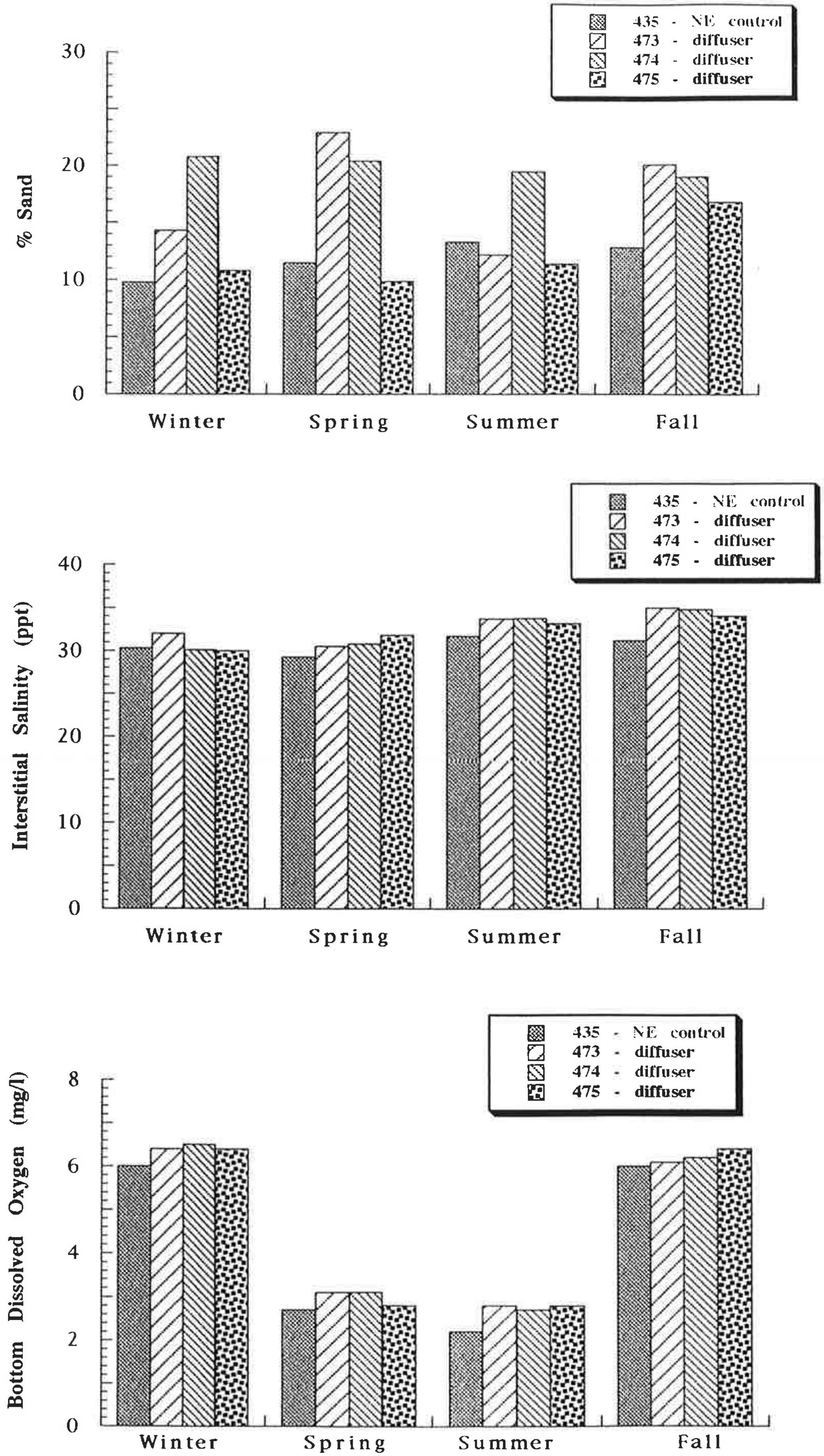
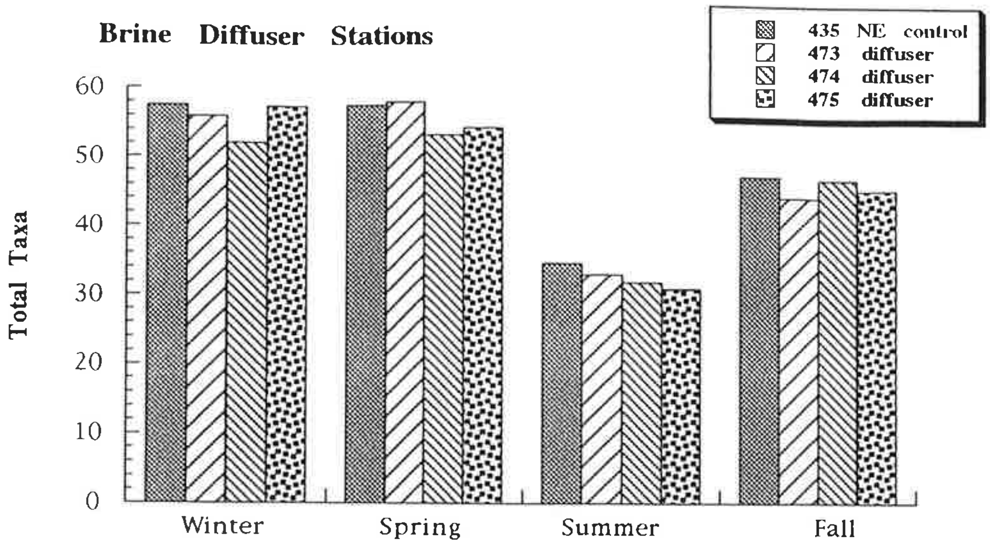
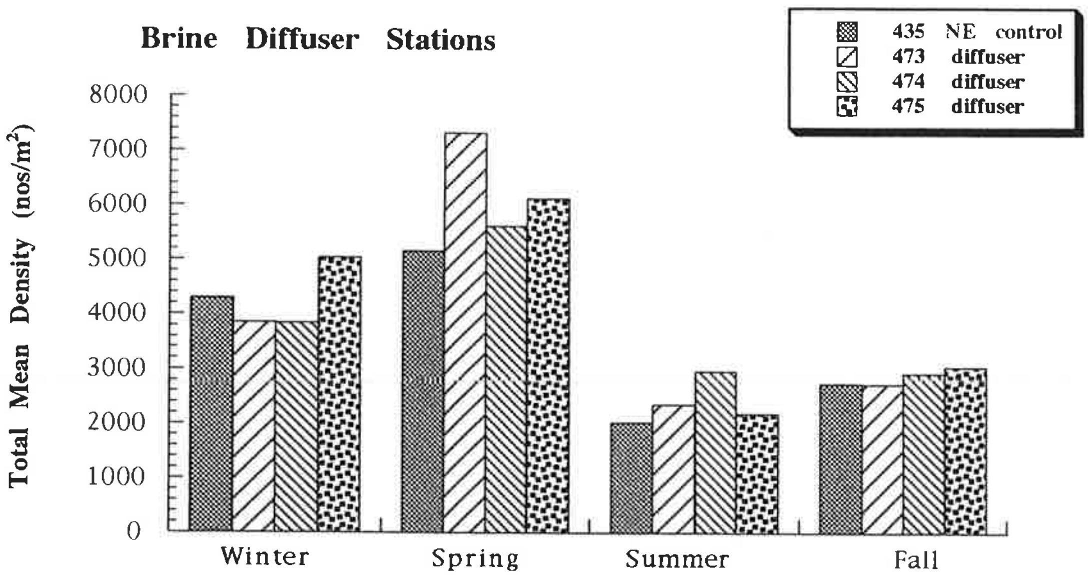


Figure 23. Seasonal summaries of hydrographic parameters over the 14-year LOOP monitoring program for the brine diffuser control and monitoring stations.





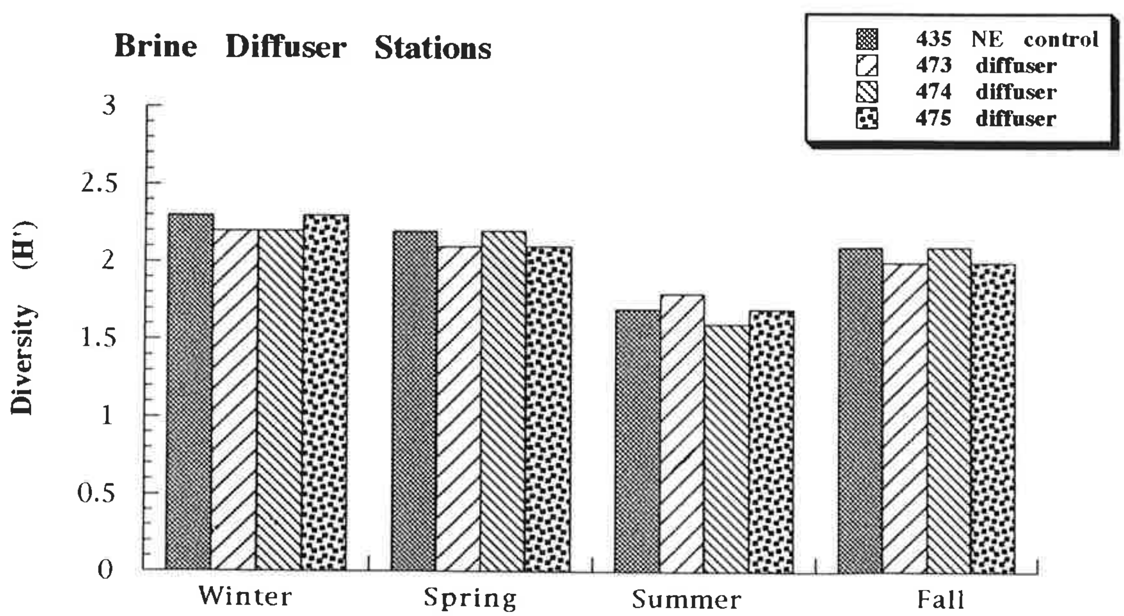


Figure 24. Seasonal summaries of characteristics of the macroinfaunal assemblage over the 14-year LOOP monitoring program for the brine diffuser control and monitoring stations.

Table 6. Results of various statistical analyses for the LOOP brine diffuser control and monitoring stations. The results of non-parametric Kruskal-Wallis comparisons of total number of taxa or mean density between stations for a given season are presented in Part A. The results of non-parametetric analyses for correlations between stations in major taxonomic groups is given in Part B. The results of non-parametetric analyses for correlations between stations in major taxa/species is given in Part C.

(A)

Season	Mean Total Taxa Chi Square	Mean Total Taxa Prob > Chi Sq	Mean Density Chi Square	Mean Density Prob > Chi Sq
Winter	1.550	0.671	1.978	0.577
Spring	1.059	0.787	0.182	0.981
Summer	0.357	0.949	0.473	0.925
Fall	1.376	0.711	1.754	0.625

(B)

Station	Variable	by	Station	Variable	Spearman Rho	Prob > Rho
435	Mollusca		435	Annelida	-0.9021	0.0000
435	Arthropoda		435	Annelida	-0.2415	0.0757
435	Arthropoda		435	Mollusca	0.0491	0.7216
473	Mollusca		473	Annelida	-0.7073	0.0000
473	Arthropoda		473	Annelida	-0.2768	0.0408
473	Arthropoda		473	Mollusca	-0.1177	0.3920
474	Mollusca		474	Annelida	-0.7413	0.0000
474	Arthropoda		474	Annelida	-0.2621	0.0532
474	Arthropoda		474	Mollusca	-0.1486	0.2789
475	Mollusca		475	Annelida	-0.7809	0.0000
475	Arthropoda		475	Annelida	-0.1955	0.1526
475	Arthropoda		475	Mollusca	-0.1071	0.4365

(C)

Station	Variable	by	Station	Variable	Spearman Rho	Prob > Rho
473	*Paraprionospio*		435	*Paraprionospio*	0.7196	0.0000
473	*Mediomastus*		435	*Mediomastus*	0.8236	0.0000
473	*Magelona*		435	*Magelona*	0.4835	0.0002
473	Rhynchocoela		435	Rhynchocoela	0.7856	0.0000

YEARLY SUMMARY OF HYDROGRAPHY

Yearly variation in hydrography for the brine diffuser control station 435 and monitoring stations 473, 474, and 475 is given in Fig. 25. There was considerable temporal variation in the percentage of sand in the sediments at all stations and ranged from near zero to 98%. The highest values for percent sand in the sediments were measured during the fall of 1985 which was less than one month after hurricane Juan moved through the monitoring area. There was little correlation between stations in the seasonal peaks in percentage of sand in the sediments (Fig. 25).

Interstitial salinities exhibited similar seasonal patterns between stations and generally varied between 20 ppt and 45 ppt (Fig. 25). In general, the brine diffuser monitoring stations had salinities which were similar to the control station. Low salinity events (< 20 ppt) occurred during 1983, 1984, 1987, and 1990 (Fig. 25).

Bottom dissolved oxygen (DO) levels showed considerable temporal variation at all stations and ranged from 0 to 10 mg/l (Fig. 25). All stations exhibited the same general pattern and magnitude of DO variation. Hypoxia and anoxia were observed at all stations (Fig. 25). The frequency and duration of hypoxia/anoxia varied considerably over the 14-year monitoring program. There were no measured hypoxic/anoxic events from the fall of 1982 to summer of 1986. From 1990 to 1993 hypoxic/anoxic events were measured during both the spring and summer seasons at all stations (Fig. 25).

YEARLY SUMMARY OF MACROINFAUNA ASSEMBLAGE

Yearly variation in general characteristics of the macroinfaunal assemblage for the brine diffuser control station 435 and monitoring stations 473, 474, and 475 is given in Fig. 26. These stations exhibited the same general temporal patterns in total number of taxa, mean density, and mean diversity. Total taxa showed considerable seasonal and yearly variation and ranged from < 5 to 100. The total number of taxa was generally highest in the winter and spring months and lowest during the summer months. Mean densities varied three orders of magnitude between season and from year-to-year and ranged from < 100 to > 22,000 individuals/m^2 indicating differential recruitment success of the macroinfaunal assemblage (Fig. 18). Densities were generally highest during the spring months and lowest during the summer. The brine diffuser stations exhibited extremely high densities during 1982, 1985, and 1988. Taxa diversity ranged from 0.5 to > 3, and was highest in the winter and spring months and lowest during the summer. The lowest values for number of taxa, density, and taxa diversity generally occurred during periods of low DO, particularly during and following hypoxic and anoxic events (see Figs. 25 and 26).

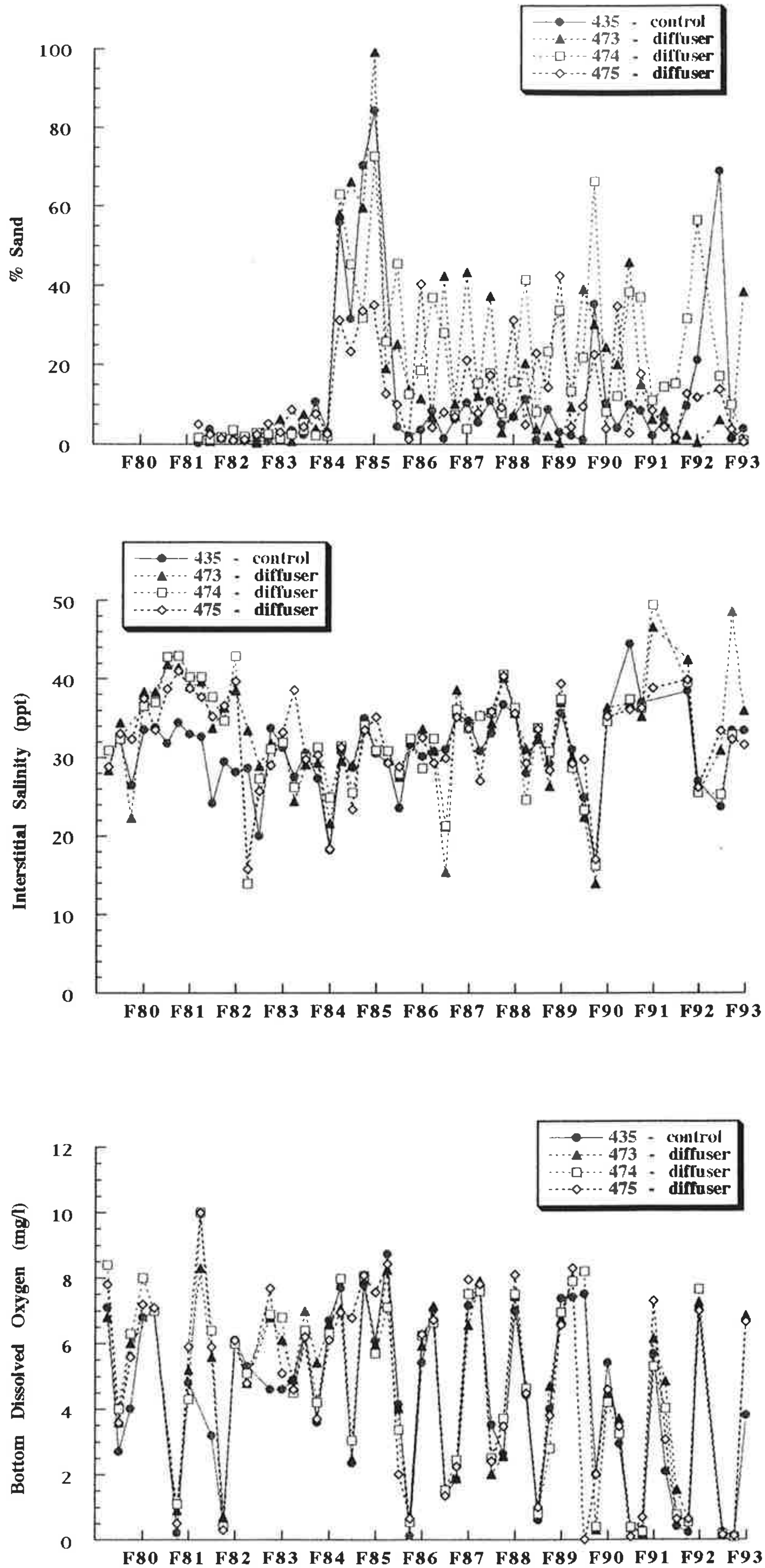
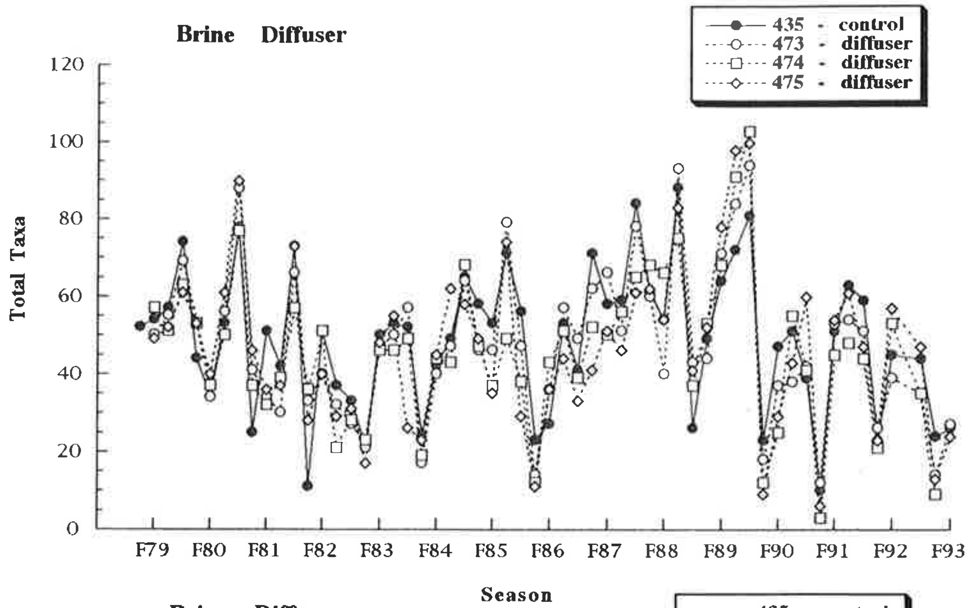
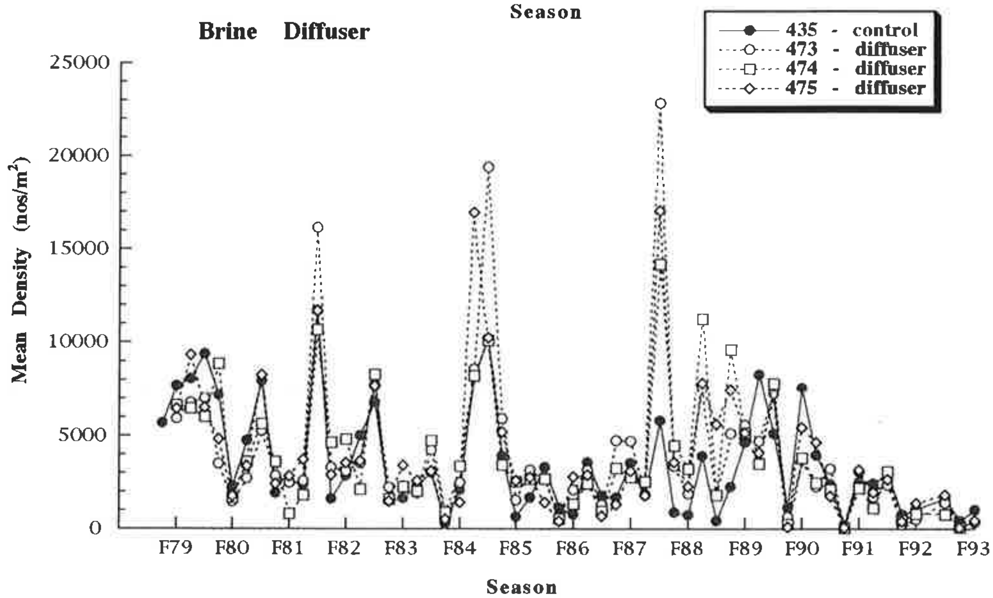


Figure 25. Yearly summaries of hydrographic parameters over the 14-year LOOP monitoring program for the brine diffuser control and monitoring stations.





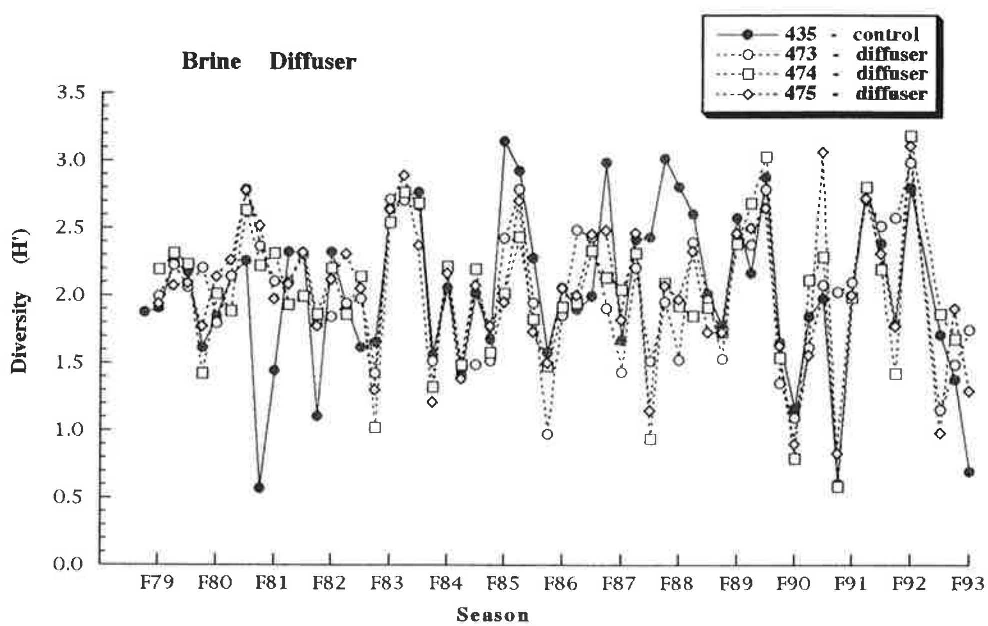
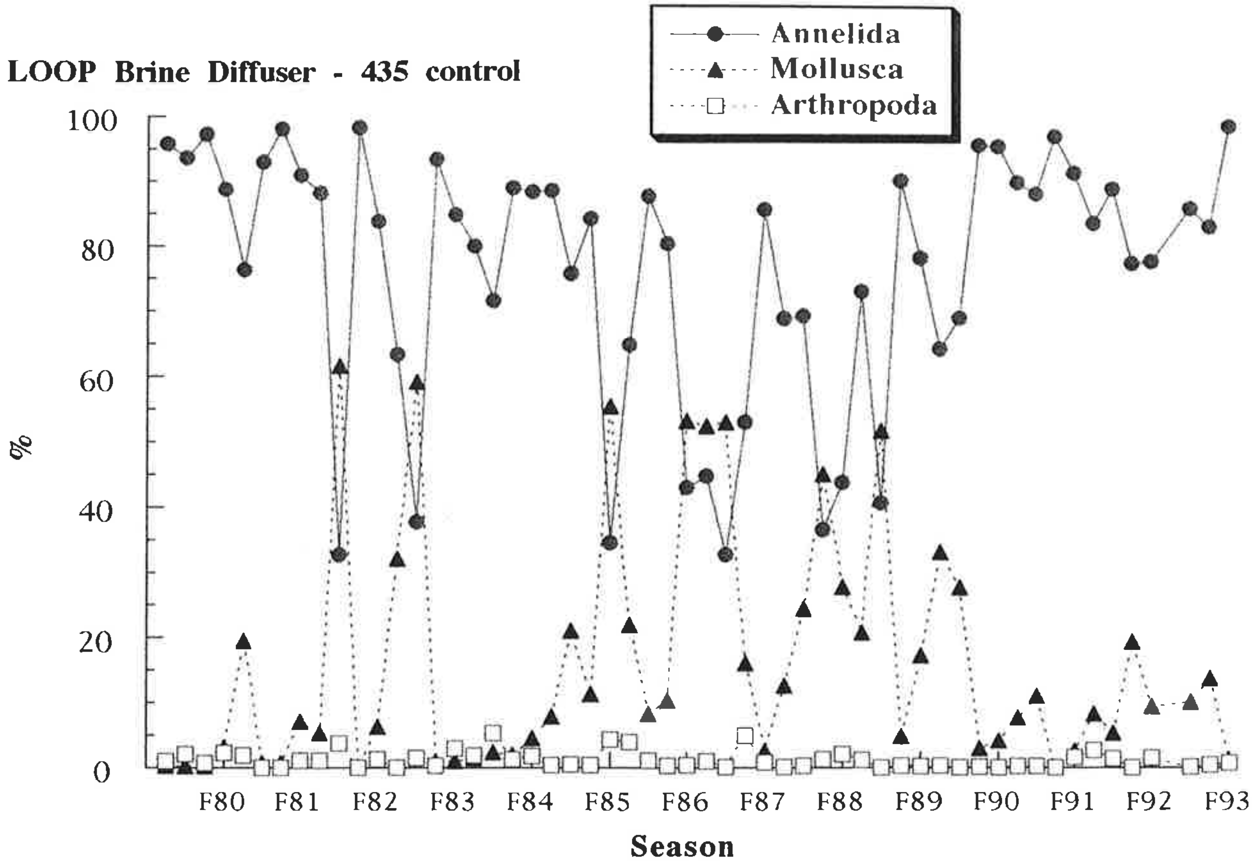


Figure 26. Yearly summaries of characteristics of the macroinfaunal assemblage over the 14-year LOOP monitoring program for the brine diffuser control and monitoring stations.

Yearly variation in abundance of the dominant taxonomic groups for the brine diffuser control station 435 and monitoring stations 473, 474, and 475 is given in Figs. 27 and 28. Polychaetes and bivalve molluscs made up > 90% of the total macroinfaunal assemblage during any given season. There were considerable seasonal differences in the percentage of the assemblage represented by these groups. In general, polychaetes dominated the assemblage at all stations. There were episodic increases in the percent abundance of bivalve molluscs resulting in shifts in dominance of the taxonomic groups during certain years (Fig. 27 and 28). There was a significant inverse correlation between the abundance of annelids and molluscs for all stations (Table 6). The increases in bivalve abundance usually occurred during the spring months and before hypoxic/anoxic events (Figs. 25, 27, and 28). Arthropods were much less abundant at these offshore stations when compared to the inland monitoring stations.

Yearly variation in abundance of dominant taxa for the brine diffuser control station 435 and monitoring station 473 is given in Figs. 29, 30, 31, and 32. The taxa/species chosen for each plot were dominant members of the macroinfaunal assemblage at these sites over the 14-year sampling effort. Taxa/species plotted were the polychaetes *Paraprionospio*, *Magelona*, *Mediomastus*, and *Sigambra*, the bivalve mollusc, *Mulinia* and the arthropods, *Corophium* and *Pinnixa* and the Rhynchocoela. There was considerable temporal variation in densities of the dominant taxa/species at these stations (Figs. 29-32). The taxa/species exhibited season-to-season and year-to-year variation in recruitment at both stations. Additionally, there was differential recruitment success for a given taxa on a yearly basis; densities often varied an order of magnitude on an annual basis. The bivalve, *Mulinia* was commonly present in very low abundance, but experienced episodic density increases and dominated the macroinfaunal assemblage during certain seasons (Figs. 29 and 31). There was no apparent correlation between density increases and season for the taxa/species, although the abundance of the bivalve, *Mulinia* was inversely related to the abundance of the polychaete, *Paraprionospio*.

Comparisons of densities of the polychaetes, *Paraprionospio*, *Magelona*, and *Mediomastus* and the Rhynchocoela for brine diffuser control station 435 and monitoring station 473 are given in Figs. 33 and 34. There was a significant positive correlation in the densities of these taxa between stations 435 and 473 (Table 6). While the patterns of taxa abundance were similar between stations, there were qualitative differences in abundance during a given season (Figs. 33 and 34). For these taxa, densities varied an order of magnitude between seasons. *Mediomastus*, and to some extent *Paraprionospio*, demonstrated consistent peaks in abundance during each year of the monitoring program. It is interesting to note that the densities for these four taxa exhibited less variation and consistently lower



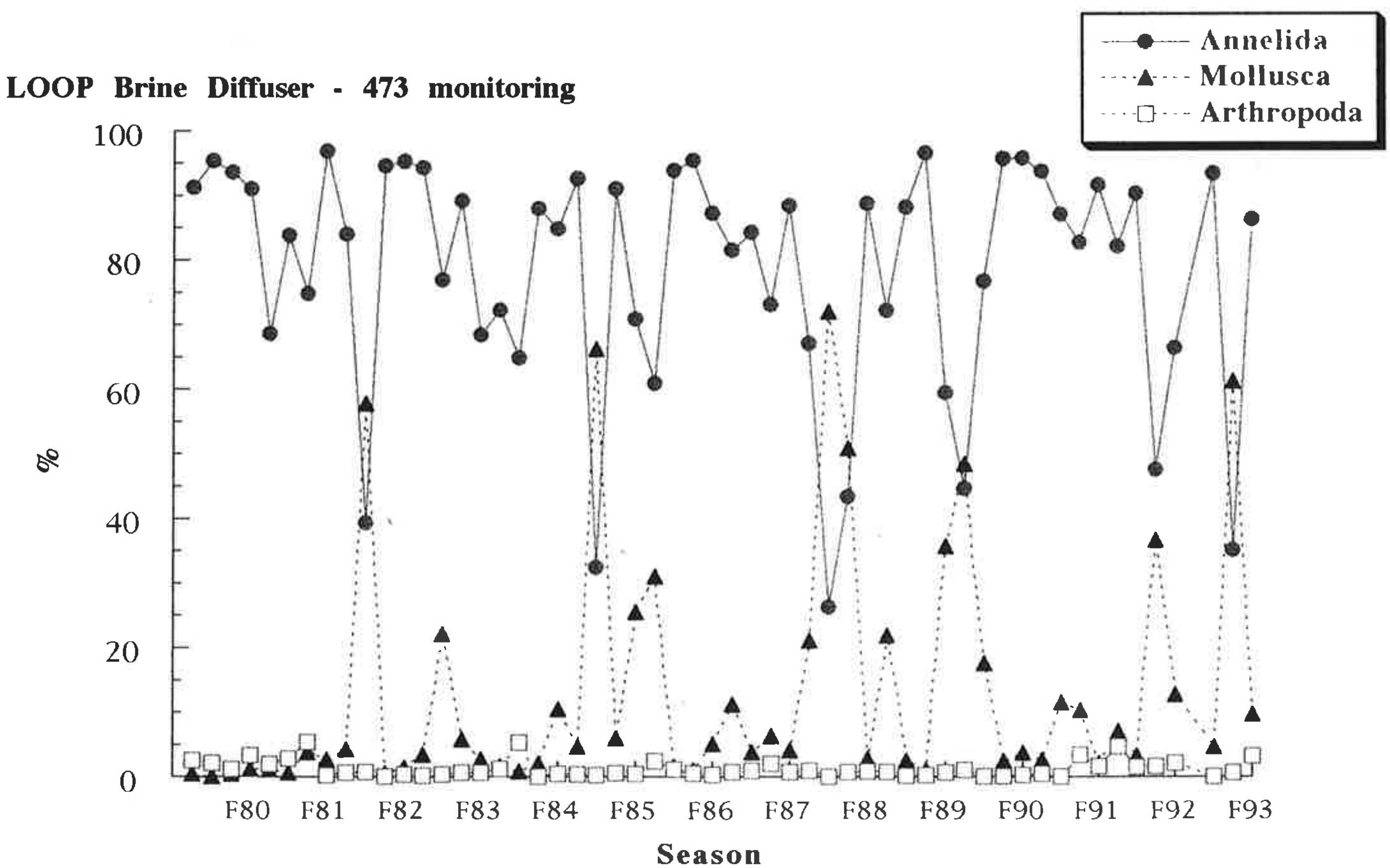
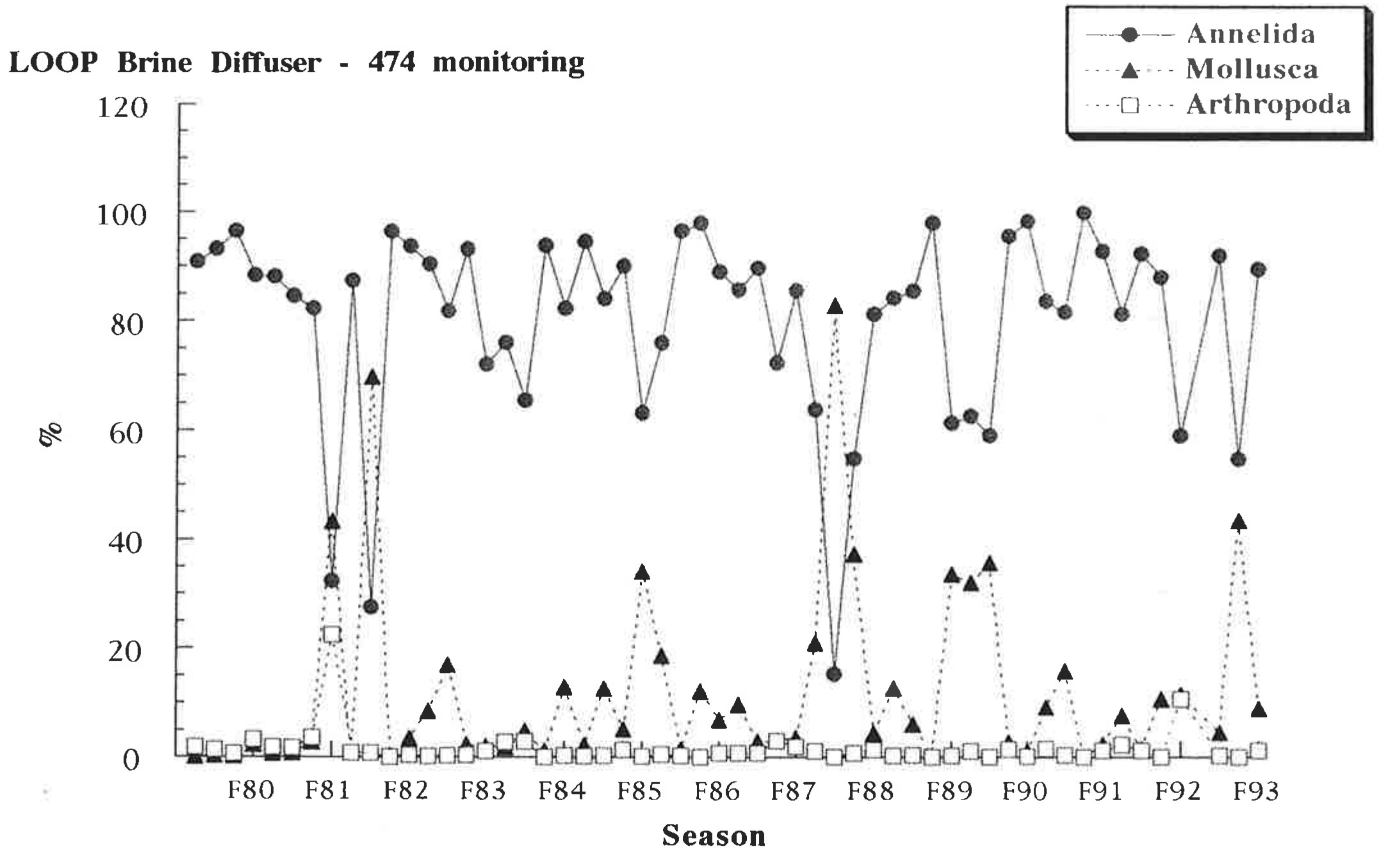


Figure 27. Yearly summaries for the percentage of the total macroinfauna assemblage represented by the major taxonomic groups, Annelida, Mollusca, and Arthropoda over the 14-year LOOP monitoring program for the brine diffuser control station 435 and monitoring station 473.



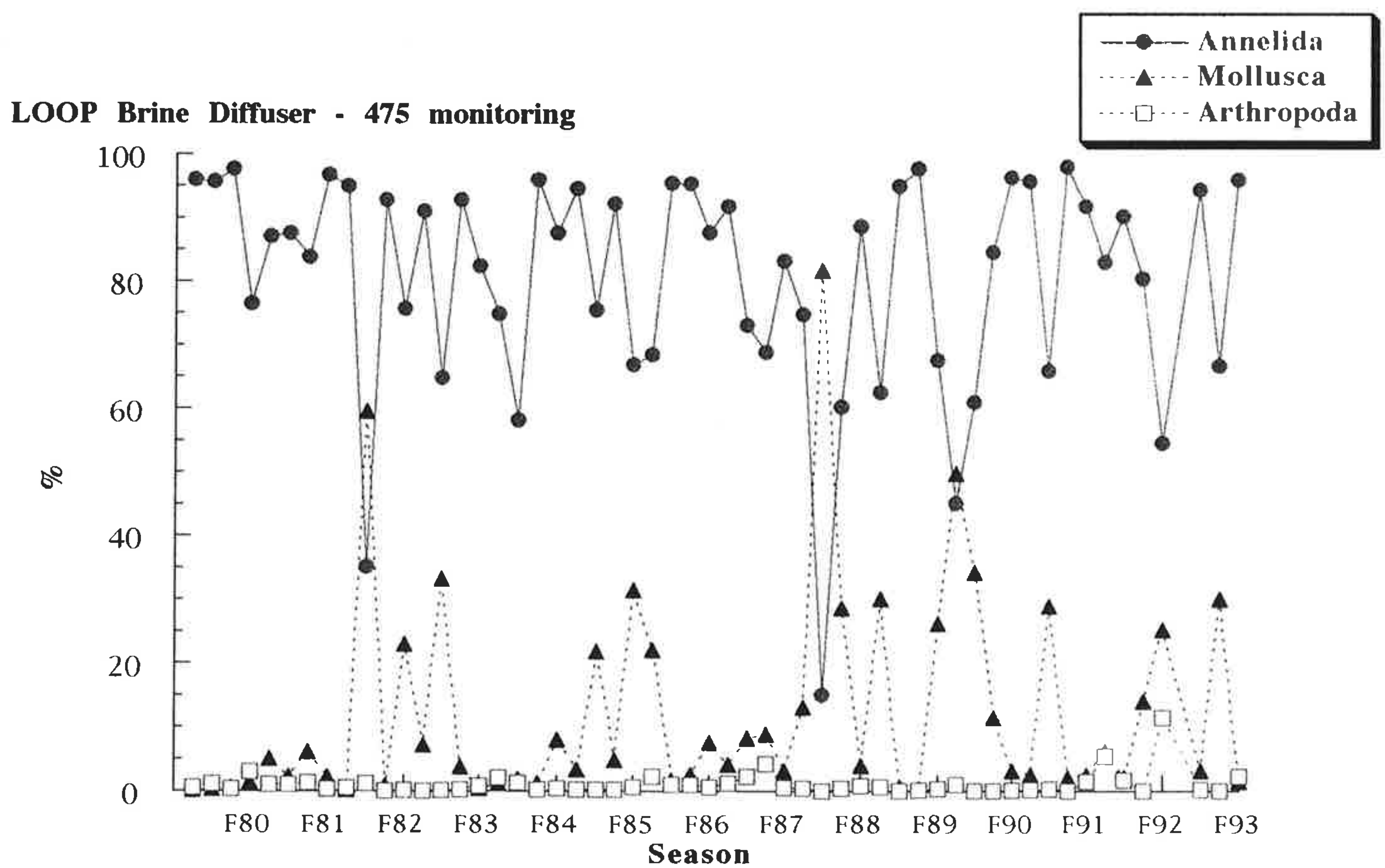


Figure 28. Yearly summaries for the percentage of the total macroinfauna assemblage represented by the major taxonomic groups, Annelida, Mollusca, and Arthropoda over the 14-year LOOP monitoring program for the brine diffuser monitoring stations 474 and 475.

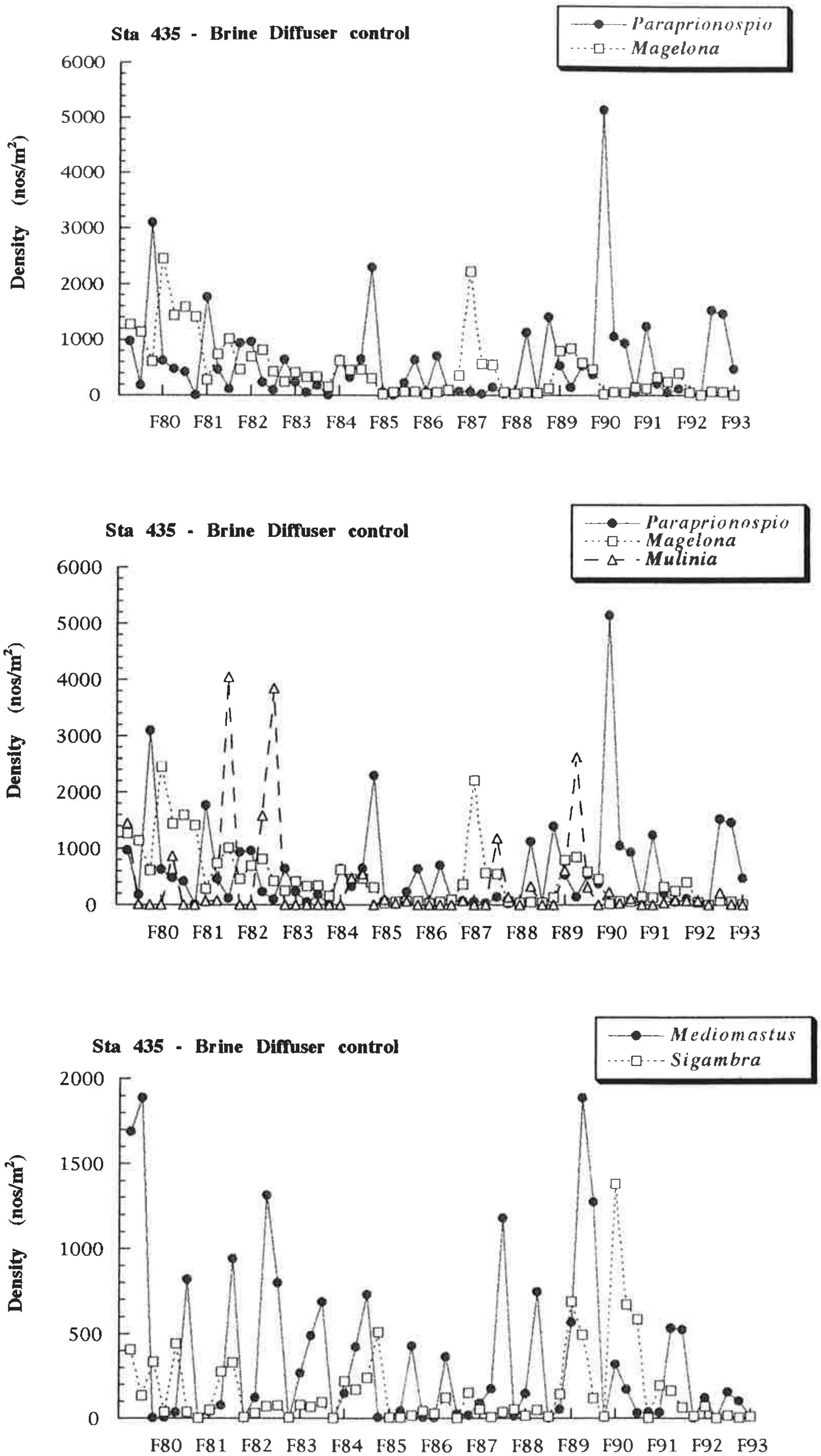
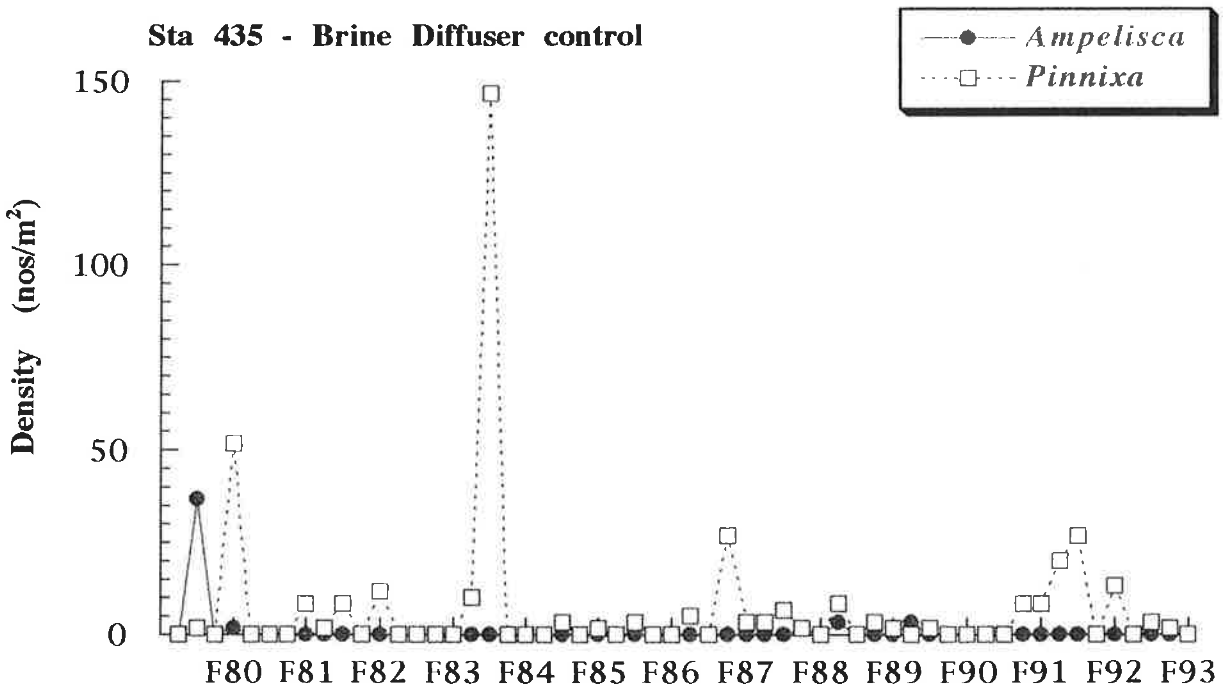


Figure 29. Yearly density summaries of the polychaetes, *Paraprionospio, Magelona, Mediomastus,* and *Sigambra*, and the bivalve mollusc, *Mulinia* for the brine diffuser control station 435.



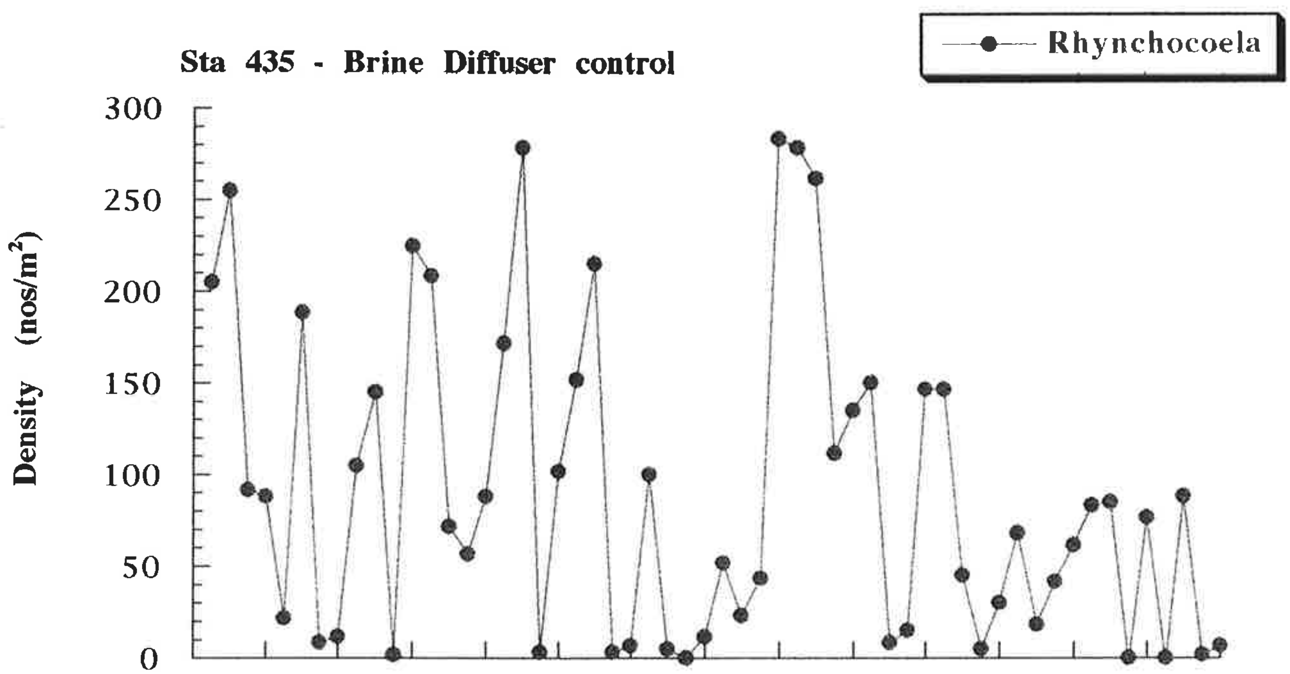
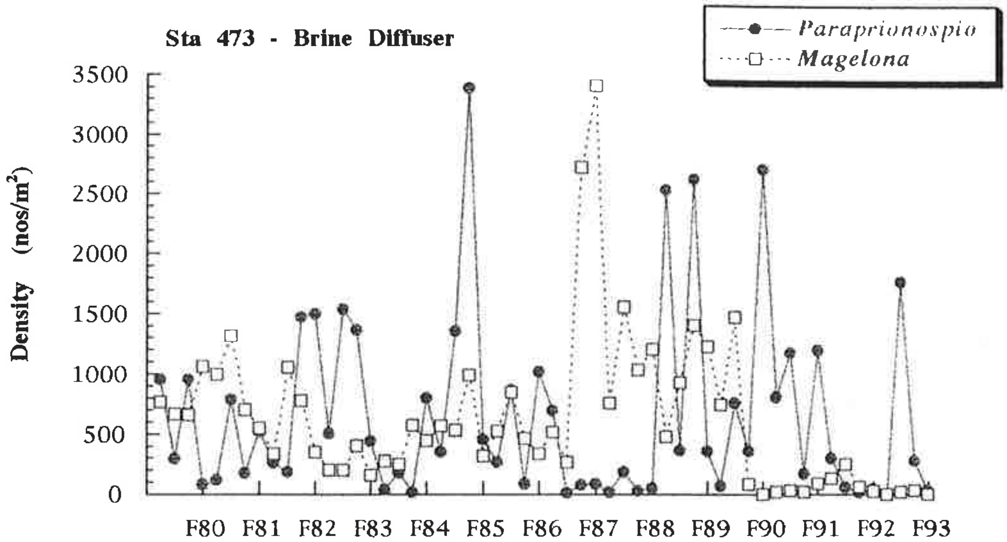
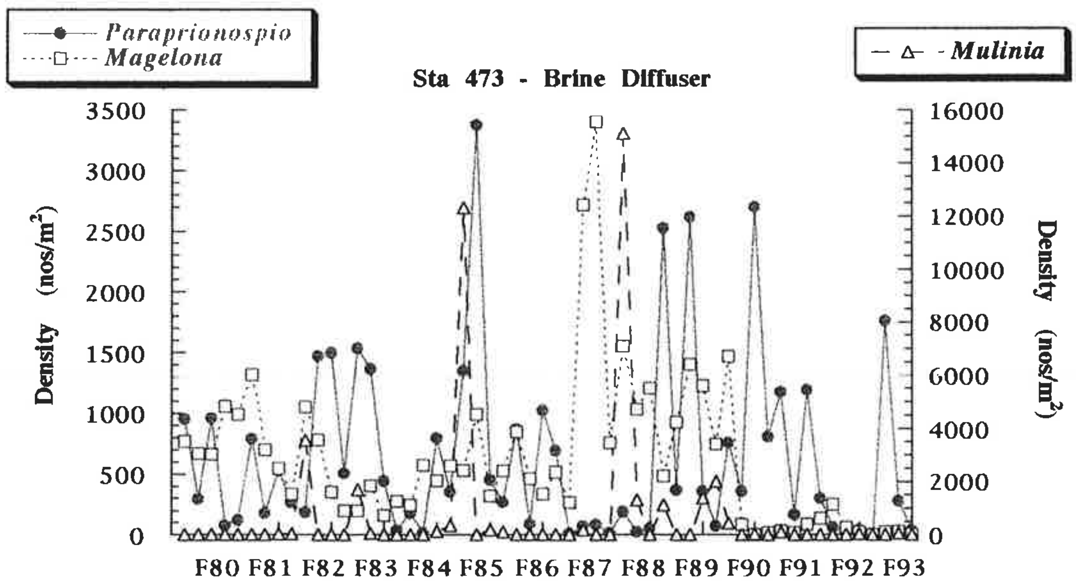


Figure 30. Yearly density summaries of the arthropods, *Ampelisca* and *Pinnixa*, and the Rhynchocoela for the brine diffuser control station 473.





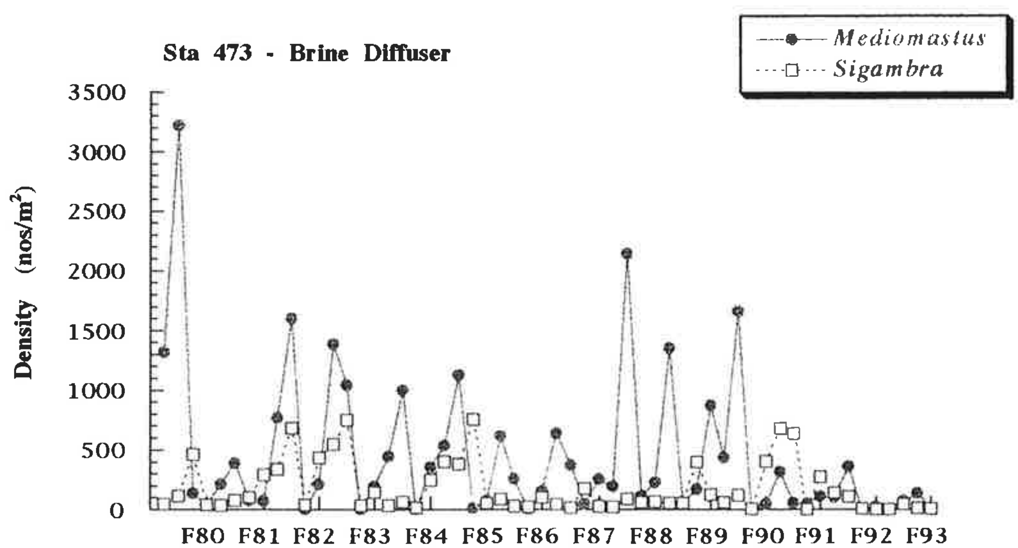
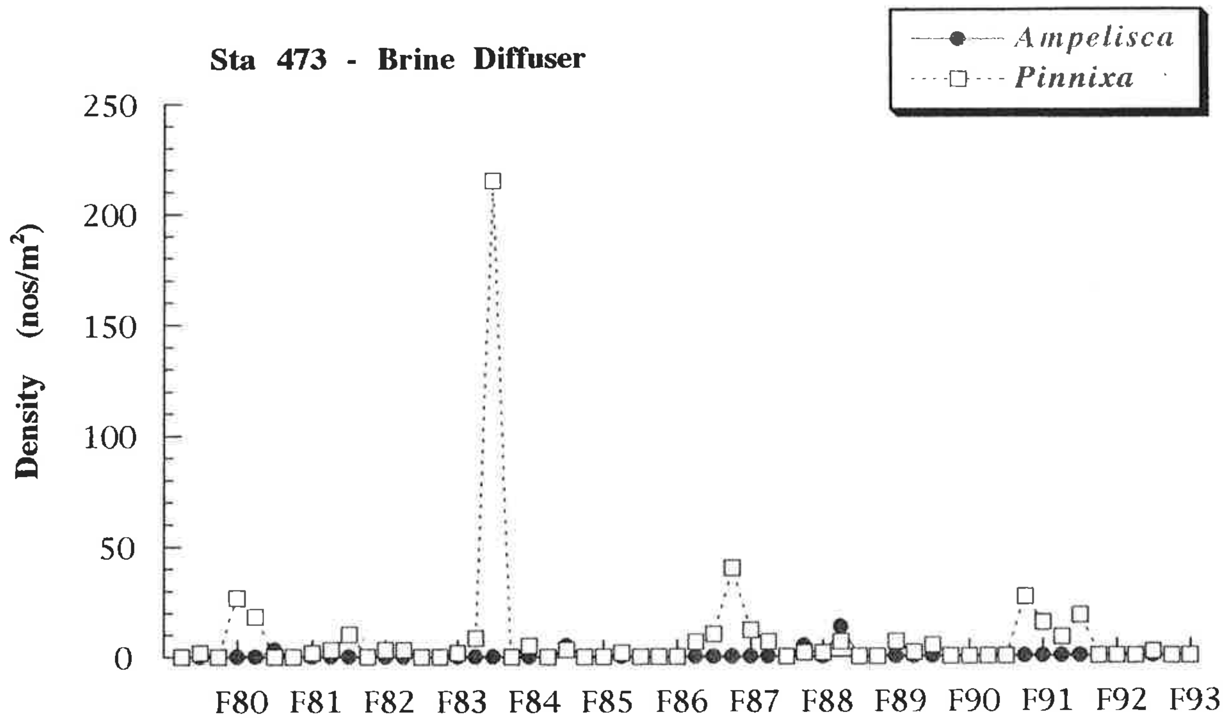


Figure 31. Yearly density summaries of the polychaetes, *Paraprionospio, Magelona, Mediomastus,* and *Sigambra,* and the bivalve mollusc, *Mulinia* for the brine diffuser control station 473.



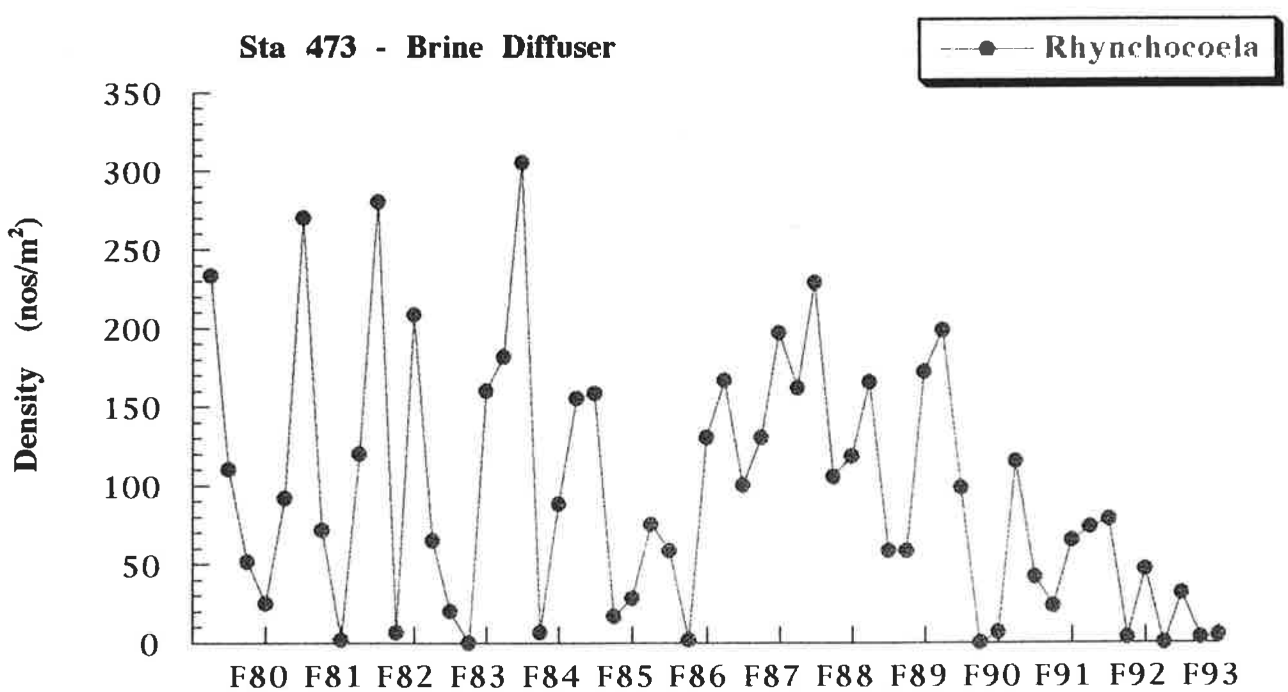
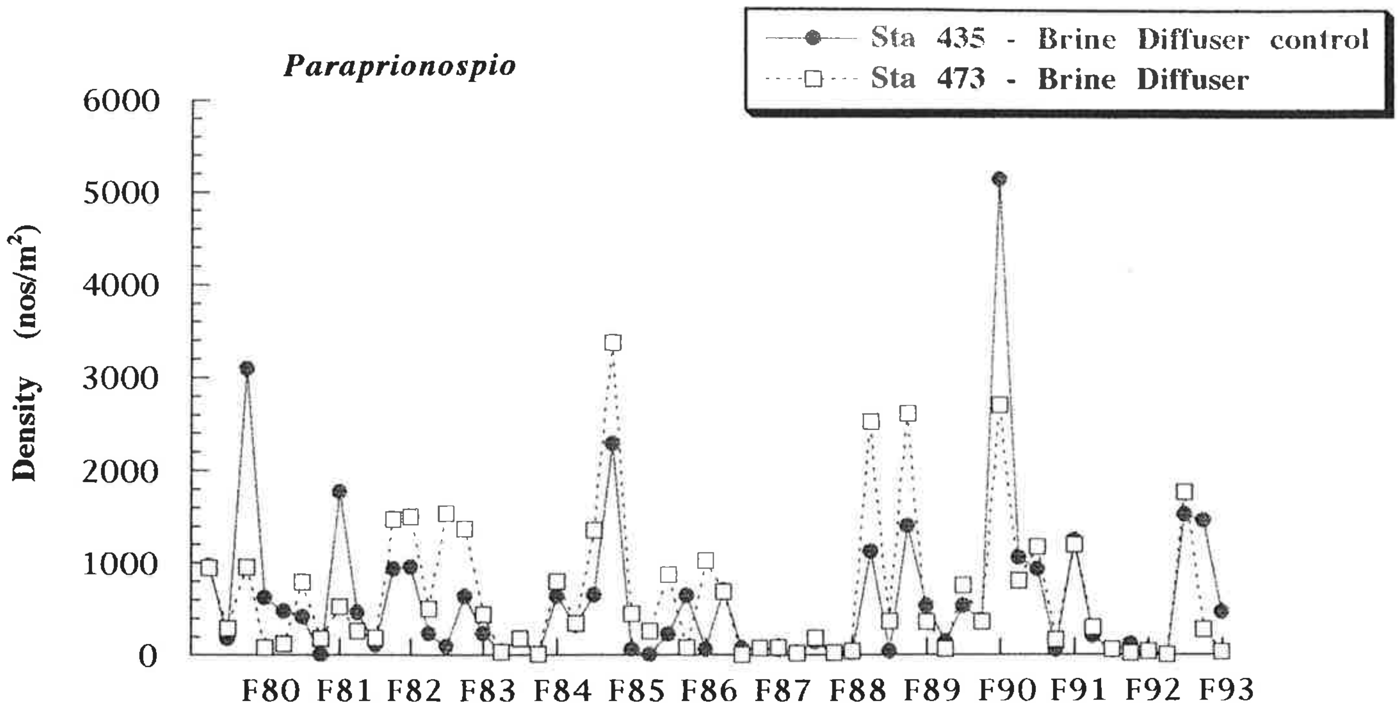


Figure 32. Yearly density summaries of the arthropods, *Ampelisca* and *Pinnixa*, and the Rhynchocoela for the brine diffuser control station 473.



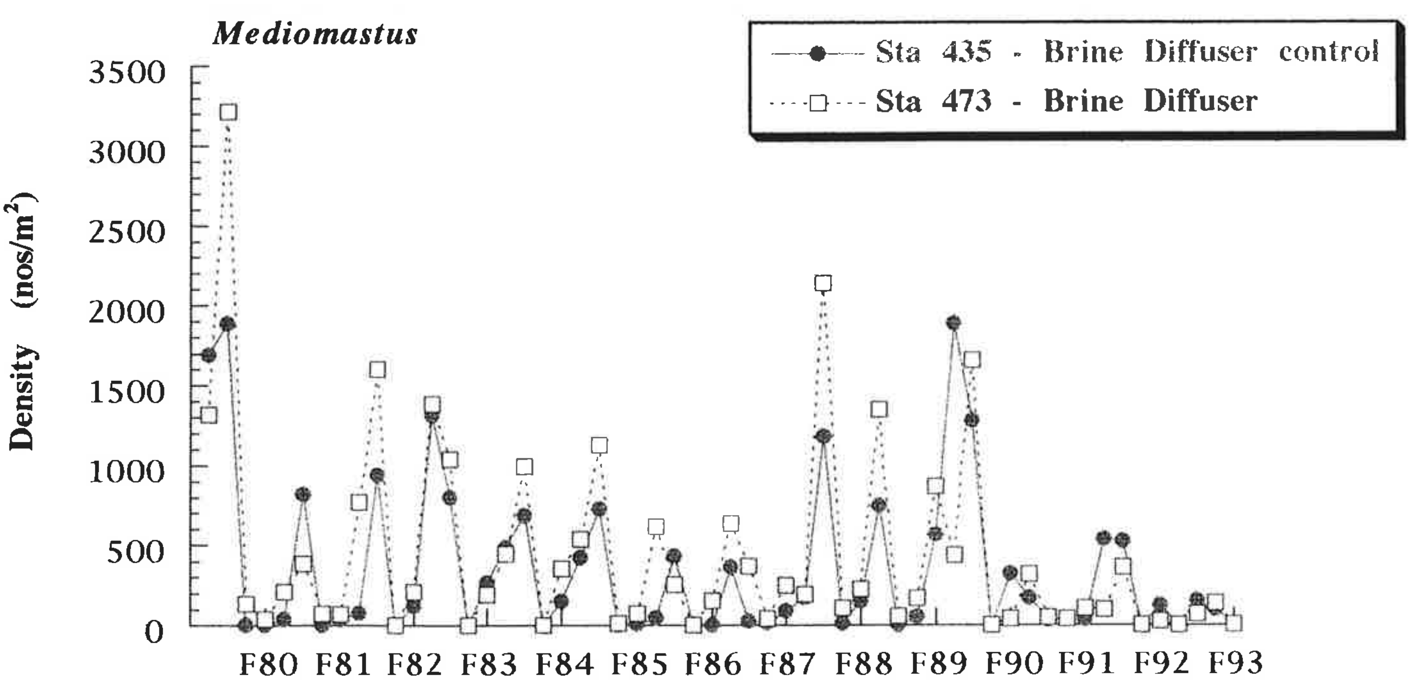
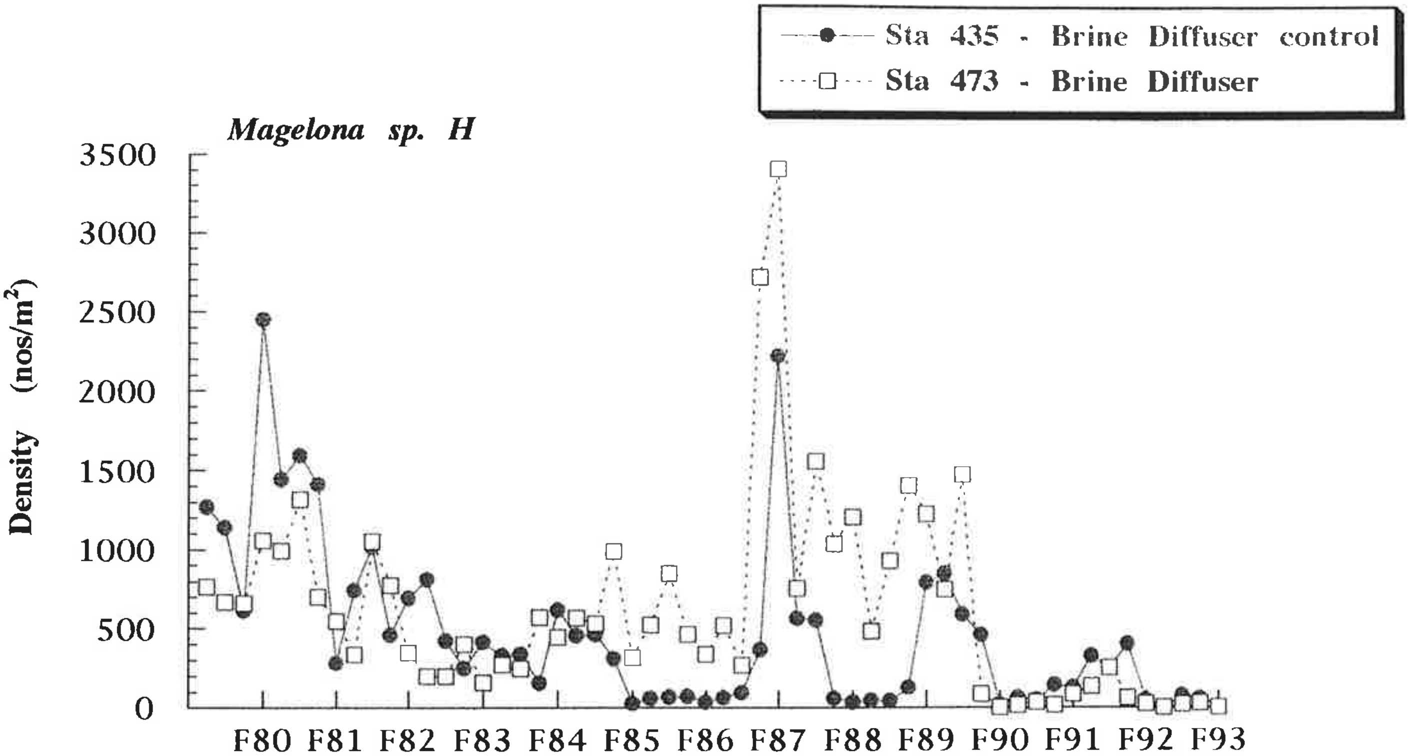


Figure 33. A comparison of yearly densities of the polychaetes, *Paraprionospio* and *Mediomastus* for control station 435 and the brine diffuser station 473.



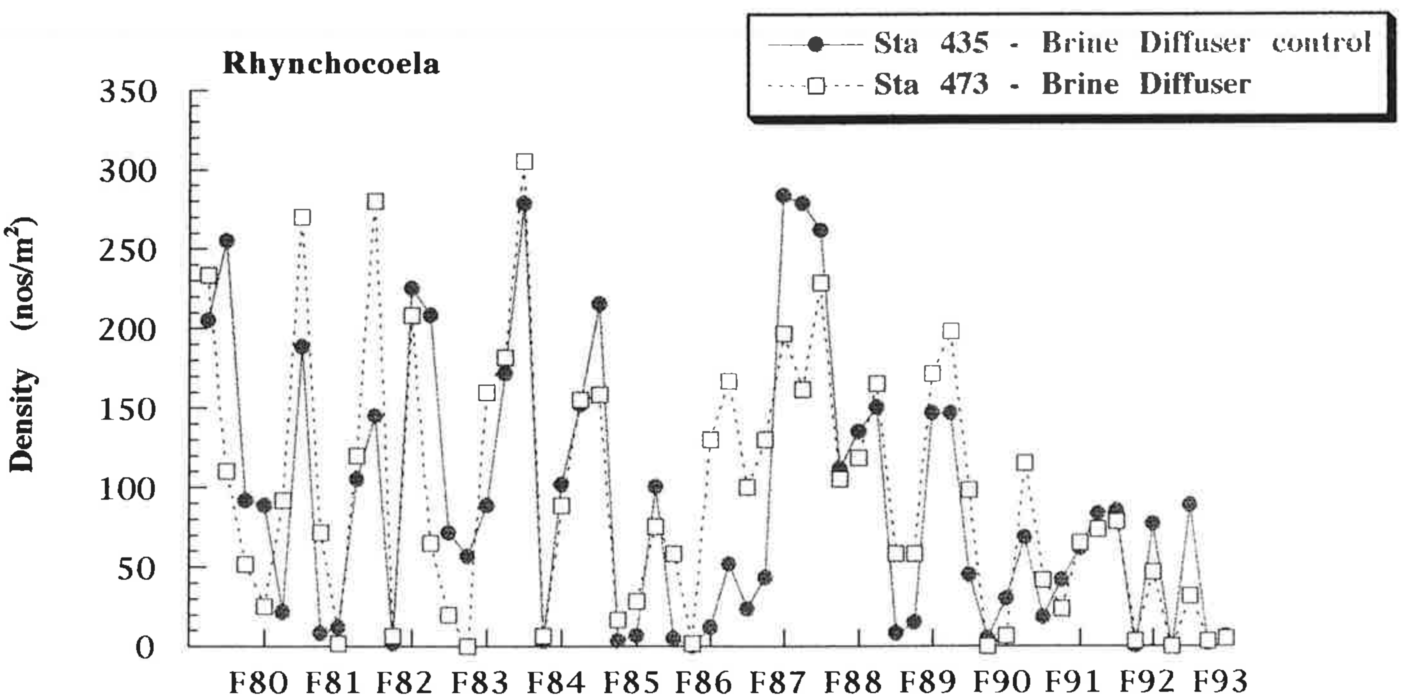


Figure 34. A comparison of yearly densities of the polychaete, *Magelona* and the Rhynchocoela for control station 435 and the brine diffuser station 473.

densities from 1991-1993. These years had hypoxic/anoxic events which were present during two consecutive sampling seasons (see Fig. 25).

RESULTS IV. OFFSHORE PUMPING STATION COMPLEX AND SPM

SEASONAL SUMMARY OF HYDROGRAPHY

A seasonal summary of hydrographic characteristics for control stations 482 and 484 and the offshore pumping station and SPM complex station 481 is given in Fig. 35. Stations 481 and 484 had, on average, four times as much sand in the sediment as station 482. The average percent sand was 27.2%, 6.4%, and 24.2% for stations 481, 482, and 484, respectively (Fig. 35). There were no spatial or temporal differences in interstitial salinity (Fig. 23). Interstitial salinity was similar at all stations during all seasons and averaged 35.4 ppt (Fig. 23). There were no differences between stations in bottom dissolved oxygen for a given season. Bottom DO exhibited considerable temporal variability. DO levels observed during the winter and spring were greater than those measured during the spring and summer (Fig. 23). DO concentrations averaged 5.5, 6.0, 4.0, and 3.2 mg/l for the winter, spring, summer and fall seasons, respectively.

SEASONAL SUMMARY OF MACROINFAUNAL ASSEMBLAGE

A seasonal summary of the general characteristics of the macroinfauna assemblage for control stations 482 and 484 and the offshore pumping station and SPM complex station 481 is given in Fig. 36. There were significant differences between average number of taxa collected during a given season (Table 7). For all seasons the number of taxa collected from control station 482 was significantly less than the number of taxa collected from stations 481 and 484. The average number of taxa collected for each station across seasons was 67.8, 39.4, and 54.0 for stations 481, 482 and 484, respectively (Fig. 36). There were significant differences between average macroinfaunal densities for a given season (Table 7). For each season, the average densities for station 481 were significantly higher than those of station 482, but not significantly different from station 484 densities. Densities ranged from 461.8 individuals/m^2 at station 482 in the winter to 2088.6 individuals/m^2 at station 481 (Fig. 36). There was minimal between station variation in diversity (H') and H' averaged 2.9, 3.1, 2.7, and 2.7 for the winter, spring, summer, and fall seasons, respectively (Fig. 36).

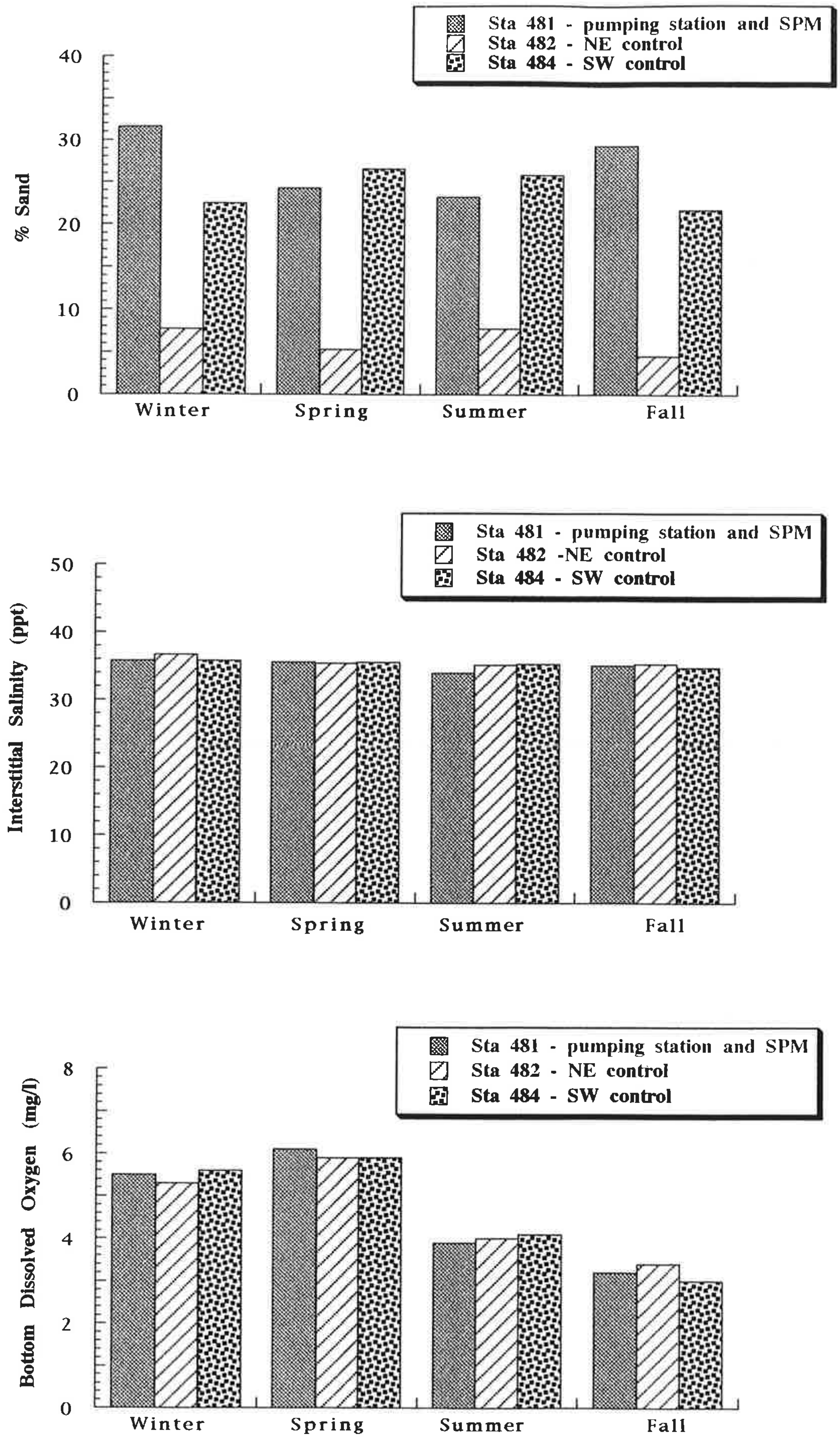


Figure 35. Seasonal summaries of hydrographic parameters over the 14-year LOOP monitoring program for the offshore pumping station complex and SPM control and monitoring stations.

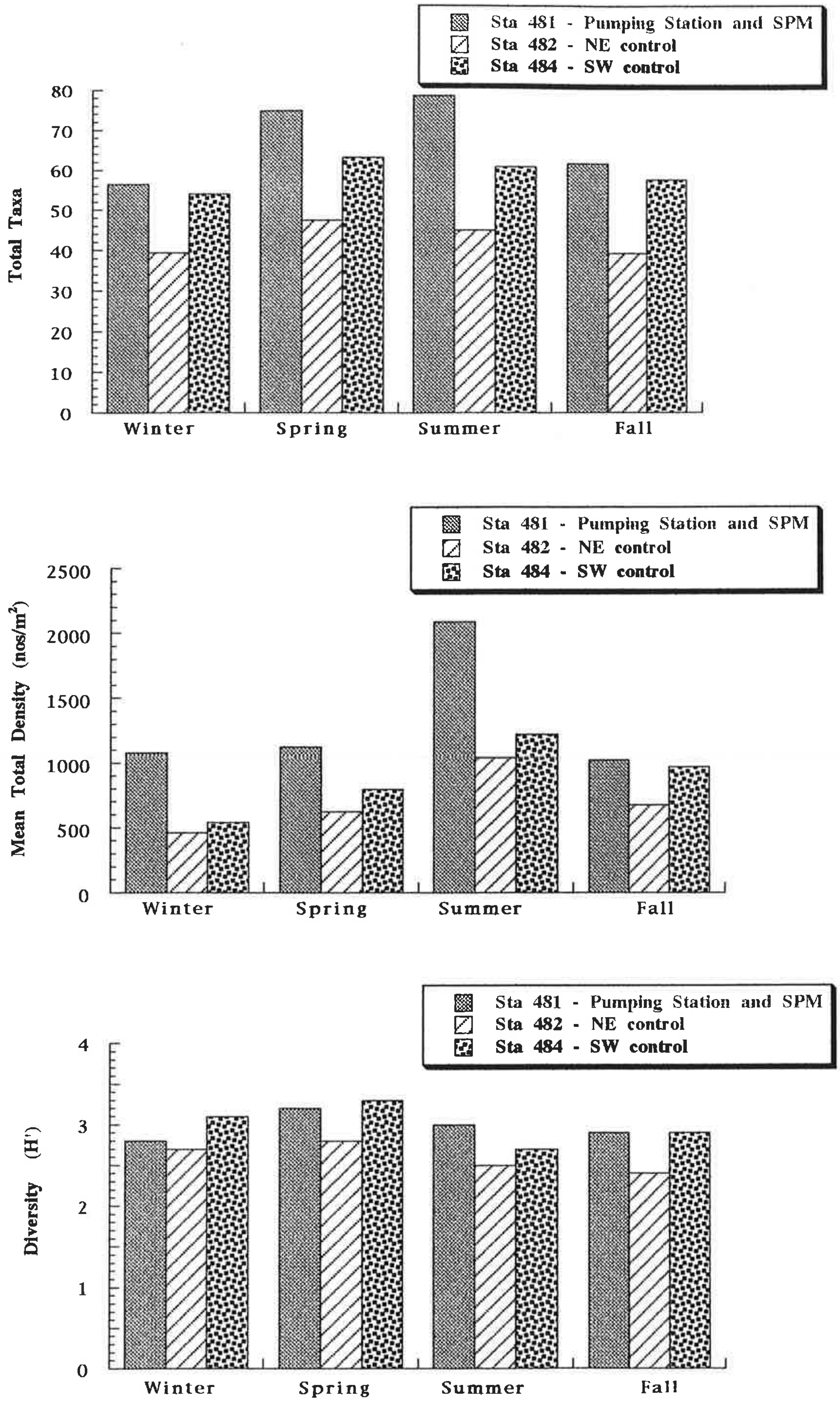


Figure 36. Seasonal summaries of characteristics of the macroinfaunal assemblage over the 14-year LOOP monitoring program for the offshore pumping station complex and SPM control and monitoring stations.

Table 7. Results of various statistical analyses for the LOOP offshore pumping station complex and SPM. The results of non-parametric Kruskal-Wallis comparisons of total number of taxa or mean density between stations for a given season are presented in Part A. The results of non-parametetric analyses for correlations between stations 481, 482, and 484 in total number of taxa between stations for a given season are presented in Part B. The results of non-parametetric analyses for correlations between stations 481, 482, and 484 in mean density between stations for a given season are presented in Part C. The results of non-parametetric analyses for correlations between stations in major taxonomic groups is given in Part D. The results of non-parametetric analyses for correlations between stations 481 and 482 in major taxa/species is given in Part E.

(A)

Season	Mean Total Taxa Chi Square	Mean Total Taxa Prob > Chi Sq	Mean Density Chi Square	Mean Density Prob > Chi Sq
Winter	10.674	0.0050	7.420	0.025
Spring	15.602	0.0004	4.346	0.114
Summer	16.009	0.0003	5.072	0.081
Fall	15.505	0.0004	6.600	0.037

(B) Taxa

Season	Stations 481/482 Spearman Rho	Stations 481/482 Prob > Rho	Stations 481/484 Spearman Rho	Stations 481/484 Prob > Rho	Stations 482/484 Spearman Rho	Stations 482/484 Prob > Rho
Winter	8.856	0.0030	0.007	0.980	6.982	0.008
Spring	13.665	0.0002	1.926	0.165	7.554	0.006
Summer	15.001	0.0001	2.384	0.123	6.327	0.012
Fall	12.015	0.0005	0.808	0.369	10.312	0.001

(C) Density

Season	Stations 481/482 Spearman Rho	Stations 481/482 Prob > Rho	Stations 481/484 Spearman Rho	Stations 481/484 Prob > Rho	Stations 482/484 Spearman Rho	Stations 482/484 Prob > Rho
Winter	6.444	0.011	3.041	0.081	1.579	0.209
Spring	4.563	0.033	0.801	0.371	1.080	0.299
Summer	4.750	0.029	1.000	0.317	1.710	0.191
Fall	6.444	0.011	0.805	0.370	2.528	0.112

Table 7. Continued.

(D)

Station	Variable	by	Station	Variable	Spearman Rho	Prob > Rho
481	Mollusca		481	Annelida	-0.8468	0.0000
481	Arthropoda		481	Annelida	-0.6283	0.0000
481	Arthropoda		481	Mollusca	0.3218	0.0188
482	Mollusca		482	Annelida	-0.4864	0.0003
482	Arthropoda		482	Annelida	-0.9193	0.0000
482	Arthropoda		482	Mollusca	0.2715	0.0493
484	Mollusca		484	Annelida	-0.8519	0.0000
484	Arthropoda		484	Annelida	-0.7401	0.0000
484	Arthropoda		484	Mollusca	0.5024	0.0001

(E)

Station	Variable	by	Station	Variable	Spearman Rho	Prob > Rho
482	*Paraprionospio*		481	*Paraprionospio*	0.7203	0.0000
482	Rhynchocoela		481	Rhynchocoela	0.6867	0.0000
482	*Pinnixa*		481	*Pinnixa*	0.3553	0.0072

YEARLY SUMMARY OF HYDROGRAPHY

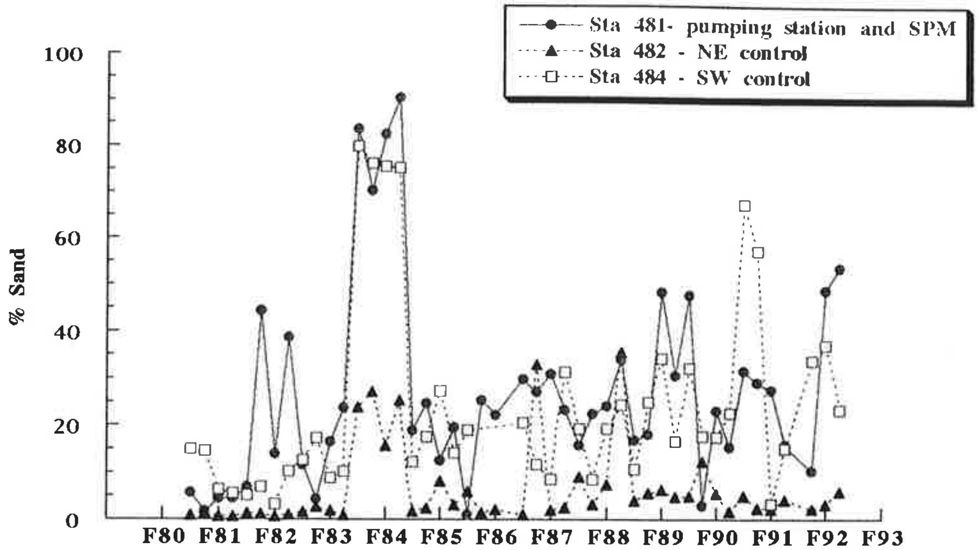
Yearly variation in hydrography for control stations 482 and 484 and the offshore pumping station and SPM complex station 481 is given in Fig. 37. There was considerable temporal variation in the percentage of sand in the sediments at all stations and ranged from near zero to > 90%. The percentage of sand in the sediments was generally less than 50% for the three stations, but values > 70% were measured during the fall of 1984 for stations 481 and 484 (Fig. 37). For most seasons, station 482 had a finer sediment texture that stations 481 and 484.

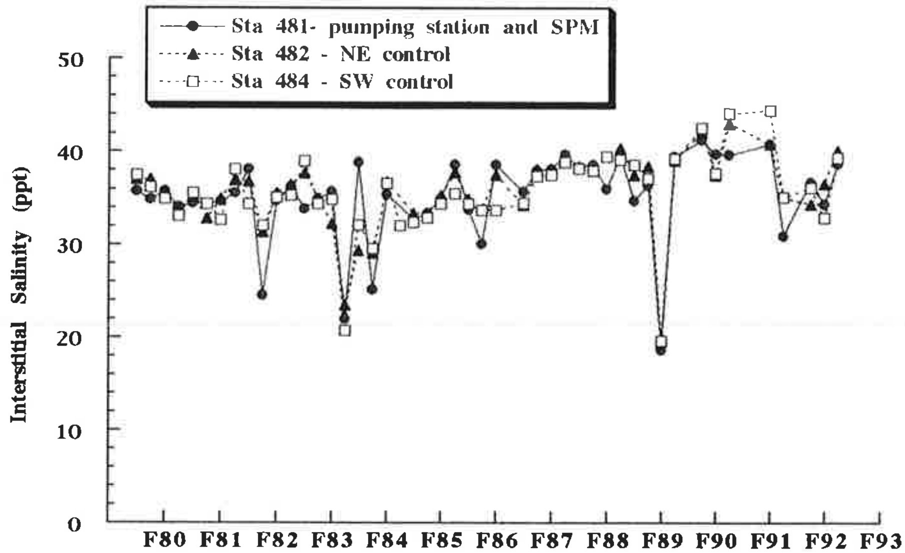
Interstitial salinities exhibited similar seasonal patterns between stations and generally varied between 30 ppt and 40 ppt (Fig. 37). In general, monitoring stations had salinities which were similar to the control station. Low salinity events (< 20 ppt) occurred during 1984 and 1989 (Fig. 37). Salinity variation at these offshore stations was less than at any other LOOP monitoring stations.

Bottom dissolved oxygen (DO) levels showed considerable temporal variation at all stations and ranged from 0 to > 12 mg/l (Fig. 37). All stations exhibited the same general pattern and magnitude of DO variation. Hypoxia and anoxia were observed at all stations (Fig. 37). The frequency and duration of hypoxia/anoxia varied considerably over the 14-year monitoring program. Hypoxia/anoxia was observed 8 out of the 14 years in the monitoring program during the summer and fall months (Fig. 37).

YEARLY SUMMARY OF MACROINFAUNAL ASSEMBLAGE

Yearly variation in general characteristics of the macroinfaunal assemblage for control stations 482 and 484 and the offshore pumping station and SPM station 481 is given in Fig. 38. These stations exhibited the same general temporal patterns in total number of taxa, mean density, and mean diversity. Total taxa for a given station showed considerable seasonal and yearly variation and ranged from < 15 at station 482 to 120 at station 481. There was at least one yearly peak in the total number of taxa for each station. The number of taxa collected from stations 481 and 484 were generally higher than at station 482. The monitoring station 481 generally had more taxa and greater seasonal variability in taxa than the two control stations (Fig. 38). Mean densities varied two orders of magnitude seasonally and from year-to-year and ranged from < 100 individuals/m^2 at station 482 to > 6,000 individuals/m^2 at station 481 (Fig. 38). Taxa diversity ranged from 1 at station 42 to > 3.5 at station 481 (Fig. 38). Peaks in taxa diversity coincided with peaks in total number of taxa. Taxa diversity at stations 481 and 484 was generally higher than diversity at station 482.





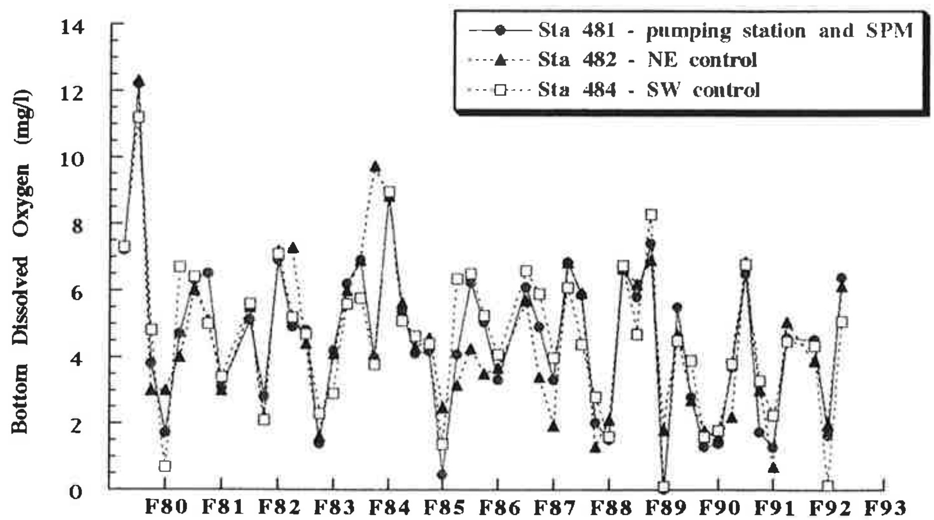


Figure 37. Yearly summaries of hydrographic parameters over the 14-year LOOP monitoring program for the offshore pumping station complex and SPM control and monitoring stations.

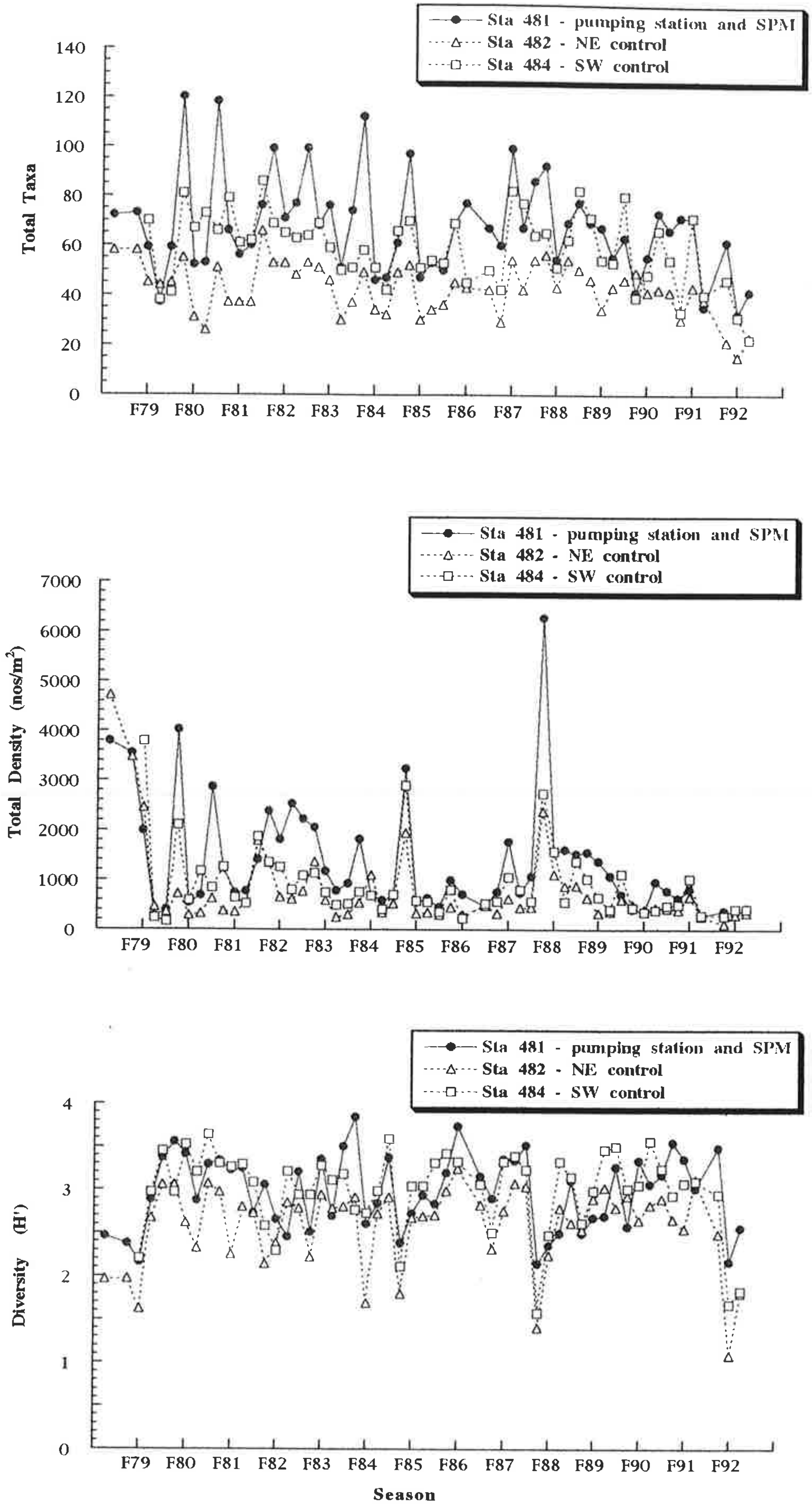


Figure 38. Yearly summaries of characteristics of the macroinfaunal assemblage over the 14-year LOOP monitoring program for the offshore pumping station complex and SPM control and monitoring stations.

Yearly variation in abundance of the dominant taxonomic groups for control stations 482 and 484 and the offshore pumping station and SPM station 481 is given in Fig. 39. Polychaetes dominated the macroinfaunal assemblage at all stations comprising from 60% to > 95% of the assemblage during most seasons. Bivalve molluscs and arthropods made up between 55% and 20% of the macroinfaunal assemblage (Fig. 39). The variability in abundance of the three taxonomic groups was similar across stations and much less than observed at other sites in the LOOP monitoring program. Additionally, the episodic increases in bivalves (particularly *Mulinia*) seen at the brine diffuser stations were absent or attenuated at these offshore stations. There was a significant inverse correlation between the percent abundance of annelids and molluscs for all stations (Table 7). There was a significant positive correlation between the percent abundance of arthropods and molluscs for all stations (Table 7).

Yearly variation in abundance of dominant taxa for control station 482 and the offshore pumping station and SPM station 481 is given in Figs. 40 and 41. The taxa/species chosen for the plots were dominant members of the macroinfaunal assemblage at these sites over the 14-year sampling effort. Taxa/species plotted were the polychaetes *Paraprionospio*, *Mediomastus*, and *Armandia*, the arthropods *Ampelisca* and *Pinnixa*, and the Rhynchocoela. There was considerable temporal variation in densities of the dominant taxa/species at these stations (Figs. 40 and 41). The taxa/species exhibited seasonal and year-to-year variation in recruitment at both stations. Additionally, there was differential recruitment success for a given taxa on a yearly basis; densities often varied several orders of magnitude on an annual basis.

Comparisons of densities of the polychaete, *Paraprionospio*, the Rhynchocoela, and the arthropod, *Pinnixa* for NE control station 482 and pumping station/SPM monitoring station 481 are given in Fig. 42. There was a significant positive correlation in the densities of these taxa between stations 435 and 473 (Table 7). While the patterns of taxa abundance were similar between stations, there were qualitative differences in abundance during a given season (Figs. 33 and 34). The densities of *Paraprionospio* were similar between stations, densities of the Rhynchocoela were generally higher at station 481, and densities of *Pinnixa* were generally higher at station 482 (Fig. 42). For these taxa, densities could vary an order of magnitude between seasons. *Paraprionospio* demonstrated a single peak in abundance of varying magnitude during each year of the monitoring program (Fig. 42).

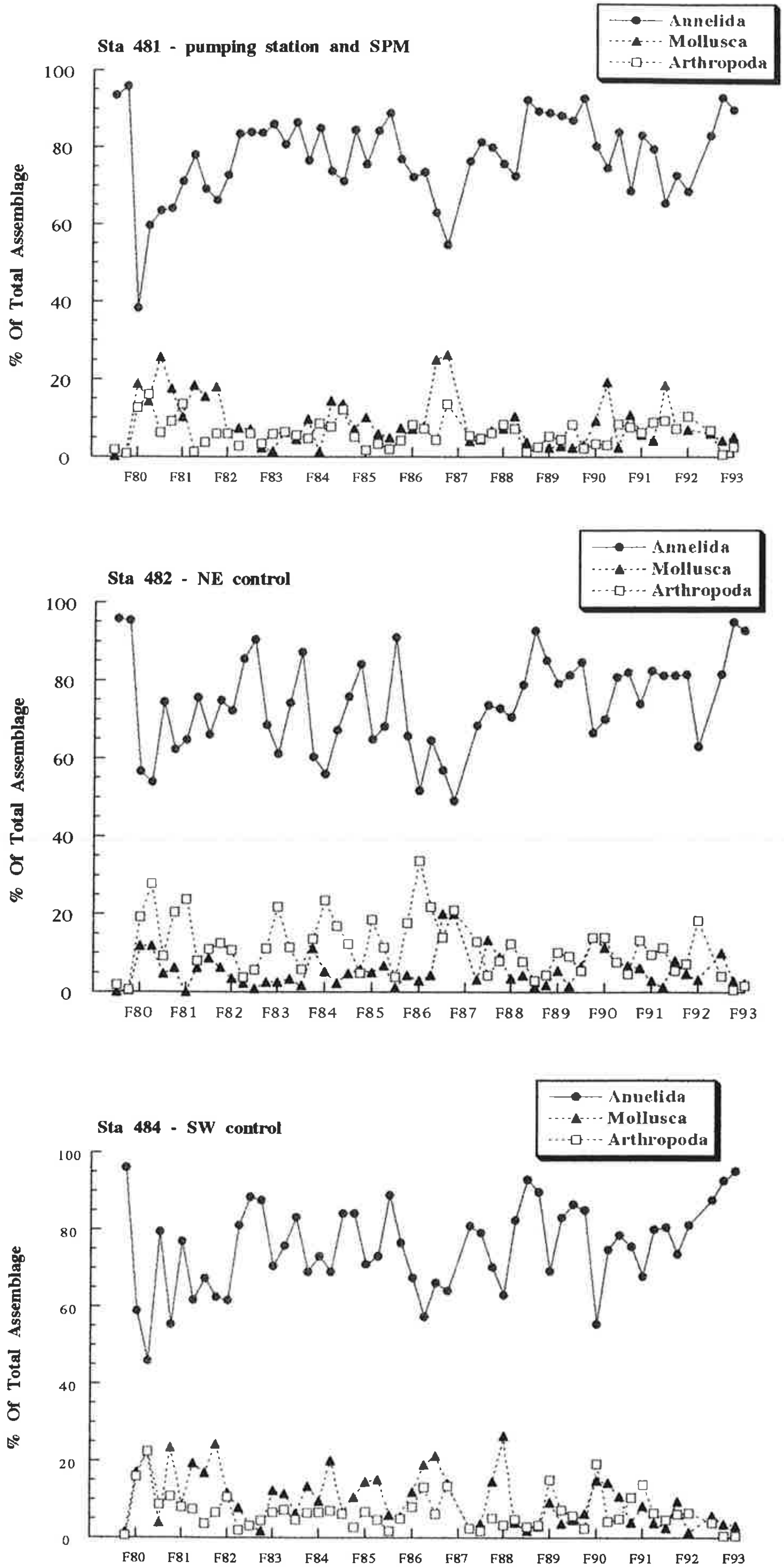
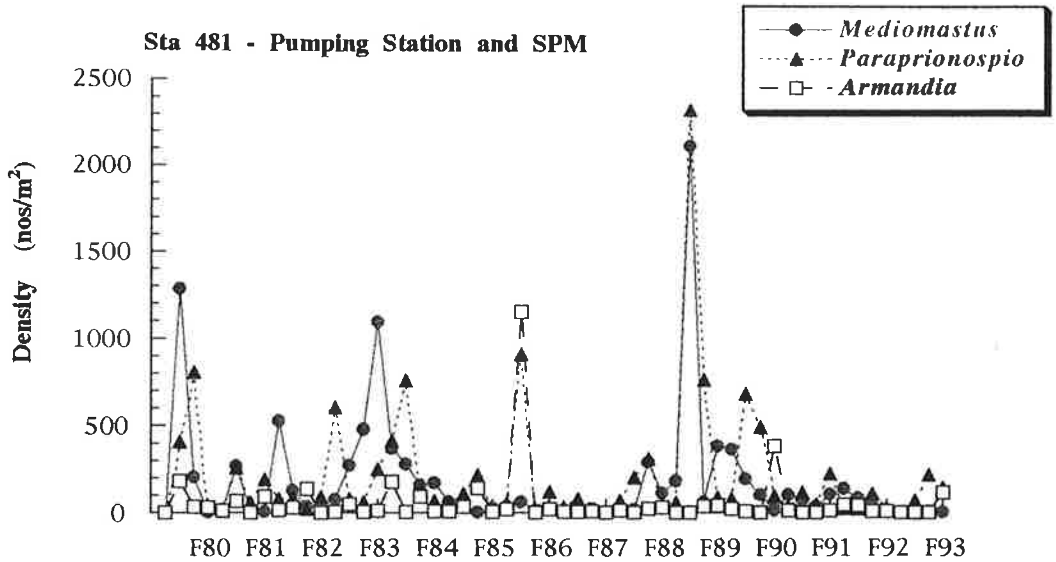
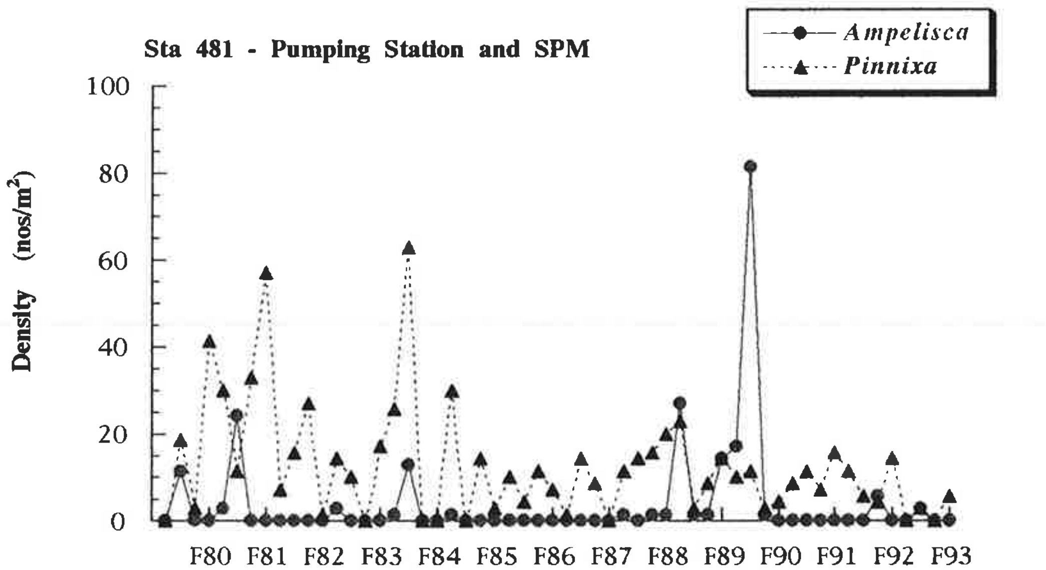


Figure 39. Yearly summaries for the percentage of the total macroinfauna assemblage represented by the major taxonomic groups, Annelida, Mollusca, and Arthropoda over the 14-year LOOP monitoring program for the offshore pumping station complex and SPM control and monitoring stations.





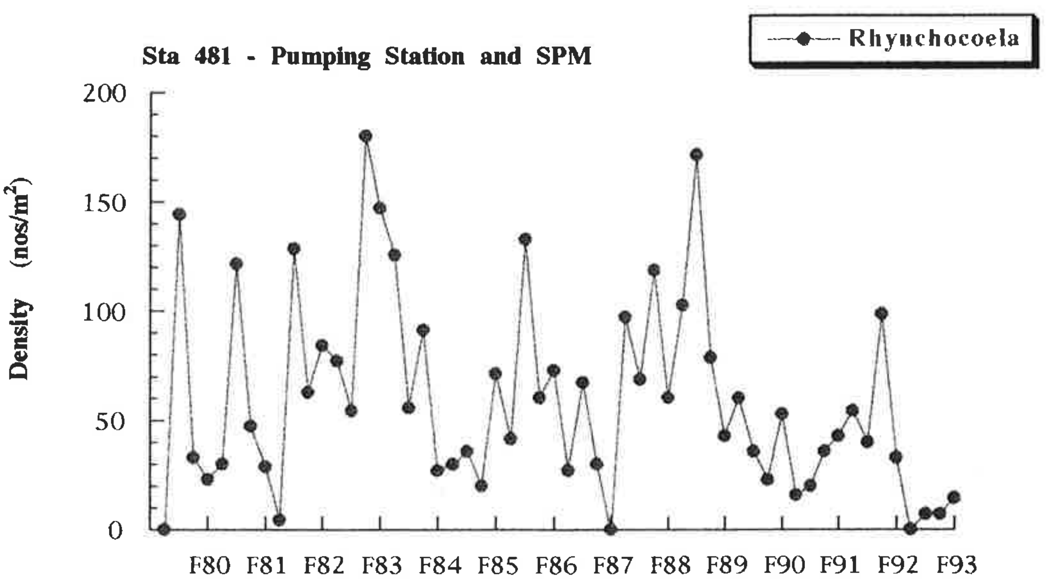
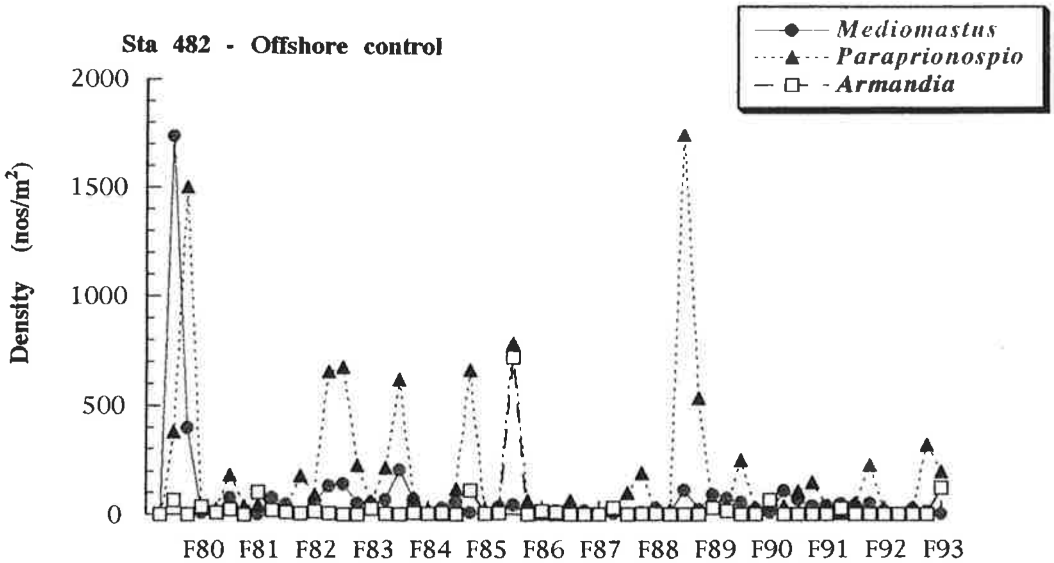
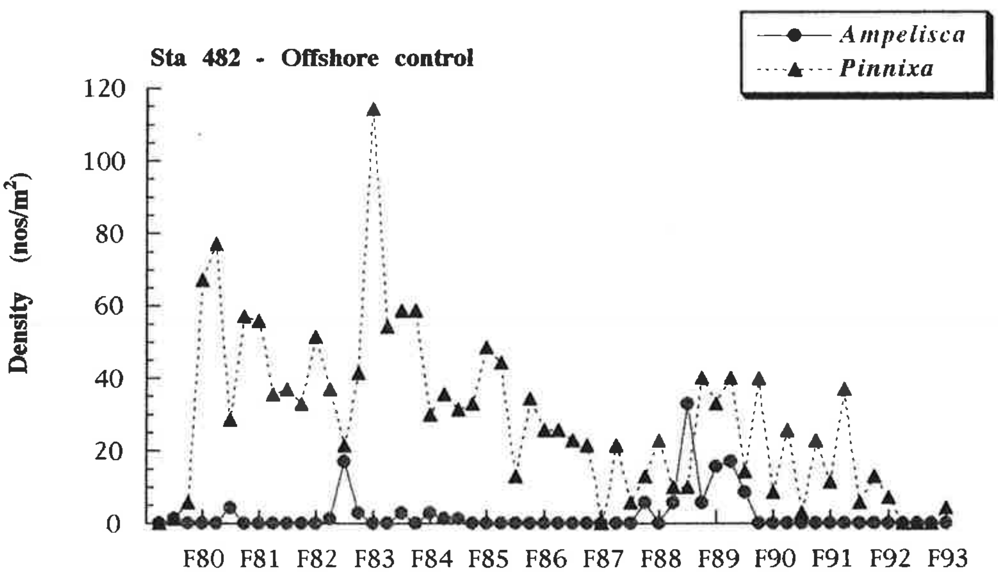


Figure 40. Yearly density summaries of the polychaetes, *Paraprionospio*, *Mediomastus*, and *Armandia*, the arthropods, *Ampelisca* and *Pinnixa*, and the Rhynchocoela for the offshore pumping station complex and SPM station 481.





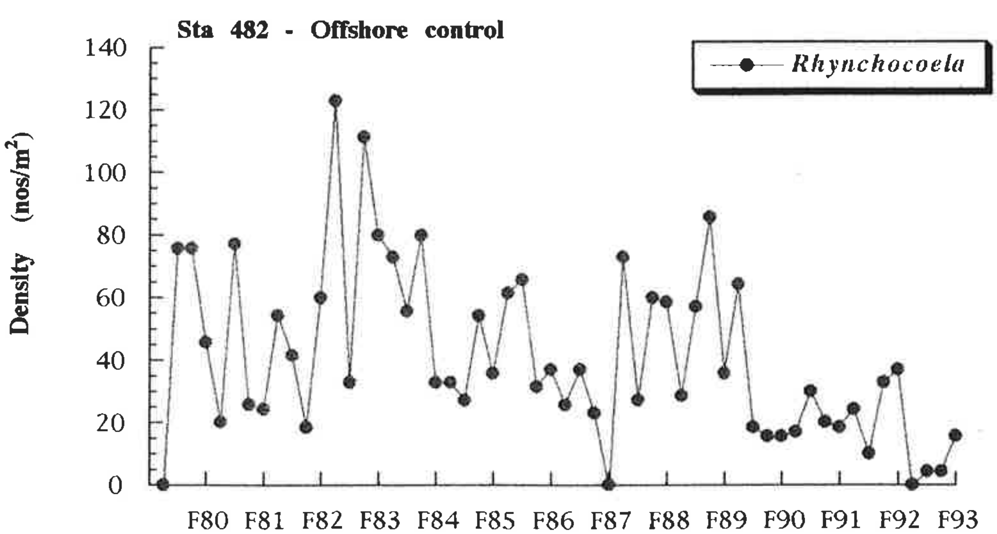
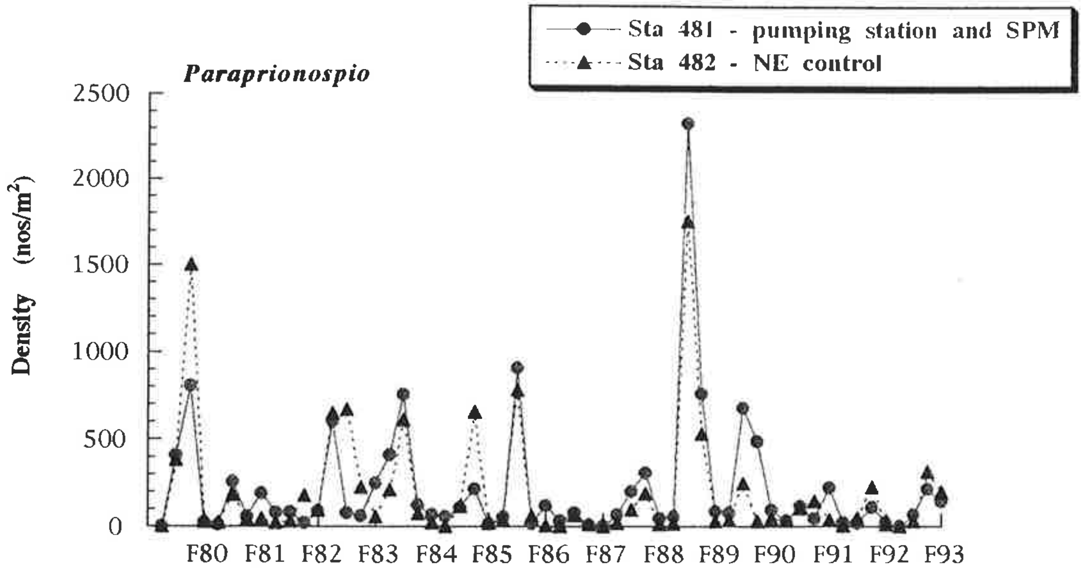
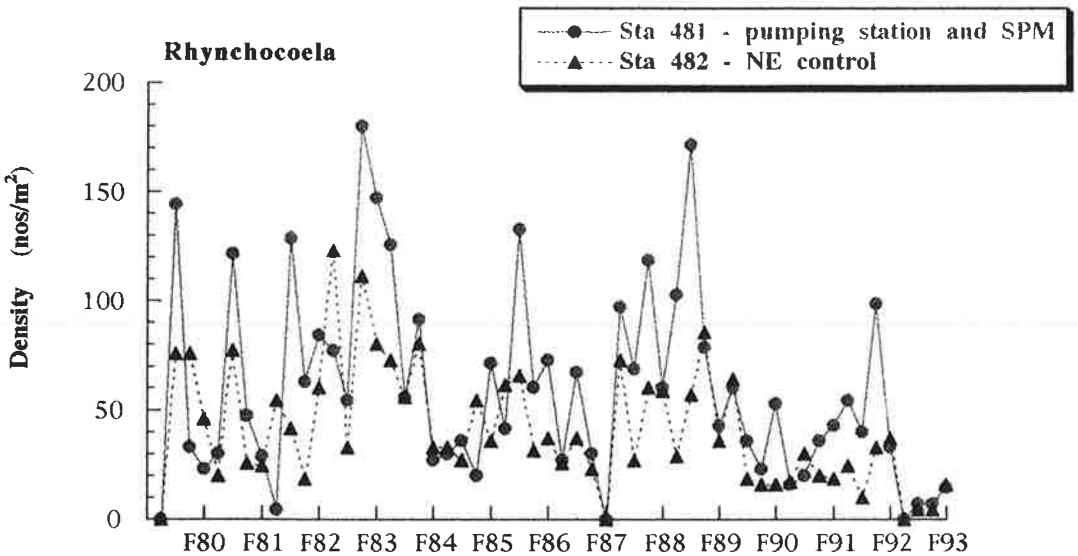


Figure 41. Yearly density summaries of the polychaetes, *Paraprionospio*, *Mediomastus*, and *Armandia*, the arthropods, *Ampelisca* and *Pinnixa*, and the Rhynchocoela for the offshore pumping station complex and SPM control station 482.





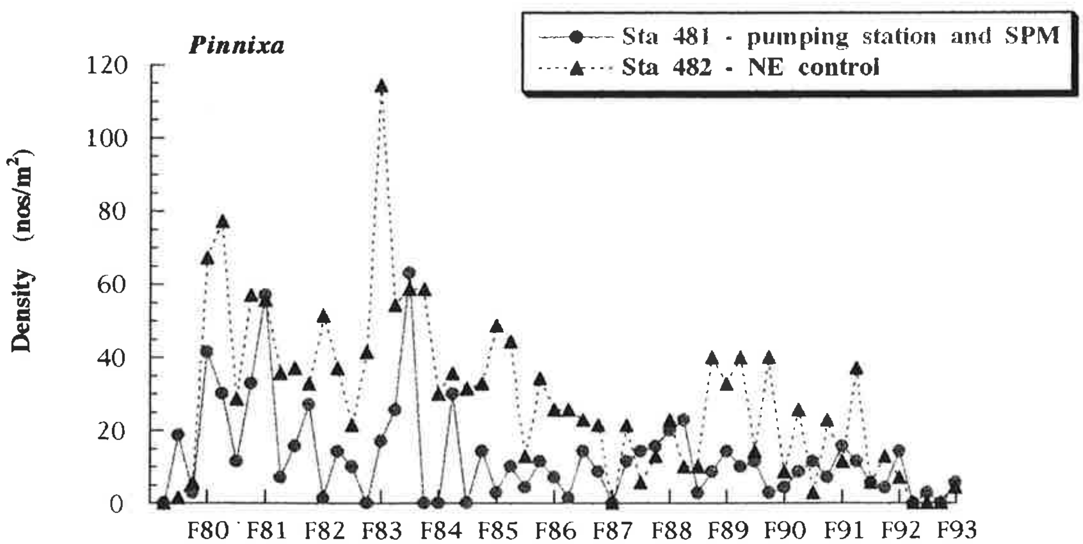


Figure 42. A comparison of yearly densities of the polychaete, *Paraprionospio*, the Rhynchocoela, and the arthropod, *Pinnixa*, for control station 482 and pumping station complex and SPM station 481.

DISCUSSION

The LOOP monitoring program comprises four ecologically distinct habitat types which are arrayed along a salinity gradient ranging from 4 ppt at the most inland stations to 35 ppt at the offshore stations. Each of these habitats exhibited seasonal and year-to-year fluctuations in hydrography and macroinfaunal assemblages over the 14 years of sampling. The macroinfaunal assemblages at each site exhibited seasonal and annual variation in the number of taxa collected, total macroinfaunal densities, numerically dominant taxa, and long-term changes in assemblage composition. Physical processes (sediment texture, salinity, dissolved oxygen availability, riverine discharge) and regional climatological patterns (tropical storms, hurricanes) influenced the structuring of benthic assemblages at these sites. However, the relative effect of the various physical factors varied considerably among the sites. The inland stations (pipeline monitoring and Clovelly/freshwater intake) were primarily influenced by riverine discharge which determined seasonal salinity levels, and to some extent, sediment texture. The nearshore brine diffuser and the offshore pumping station complex/SPM stations were primarily influenced by seasonal shifts in dissolved oxygen availability, particularly hypoxic and anoxic events.

There were no significant differences in total number of taxa and total densities between control and monitoring stations at the inland pipeline monitoring site, the Clovelly/freshwater intake site, or the brine diffuser site on a seasonal basis. There were significant differences between the total number of taxa and total densities at the offshore site. These differences were due to the fact that control station 482 had different sediment characteristics when compared to control station 484 and monitoring station 481. However, total number of taxa and total densities at monitoring station 481 and control station 484 were not significantly different. There were also significant correlations at stations from each site between hydrographic and macroinfauna characteristics over the 14-year monitoring period. The data also indicated consistently similar patterns in abundances of major taxonomic groups, dominant taxa, and changes in macroinfauna assemblage composition. It is interesting to note that many of the patterns seen in the LOOP dataset were apparent only when considering multiple years of information. Any given one- or two-year period exhibited dramatically different hydrographic and macroinfaunal assemblage characteristics.

The macroinfaunal assemblages seen at the four LOOP sites were similar in structure to other North American marine benthic communities in similar habitat types. The hydrographic patterns and macroinfaunal assemblages were similar in function to estuarine and offshore benthic communities described from the northern Gulf of Mexico. The dynamics of benthic communities in the northern Gulf of Mexico are dominated by two unique interacting physical processes: 1) discharge from the Mississippi and Atchafalaya Rivers; and 2) regular seasonal occurrence of natural hypoxia and anoxia. These two physical processes are responsible for the dramatic variation seen in the abundance and species composition of benthic macroinfaunal assemblages in the northern Gulf of Mexico.

Boesch (1972) reported a gradient of decreasing benthic community diversity from the polyhaline regions of an estuary to the shallow continental shelf at Hampton Roads, Virginia. Sediment texture and pollution also contributed to structuring these benthic communities. Boesch (1973) also found that benthic community structure exhibited considerable spatial and temporal variation in the Hampton Roads estuary. Species associations were dependent upon substrate type and season and reflected the relative abundance of ubiquitous species and species that were only seasonally abundant.

McCall (1977) studied the nearshore macroinfaunal assemblage of Long Island Sound and reported that it was characterized by a highly variable species composition. Some species underwent large spatial and temporal fluctuations in local abundance while other taxa varied little. Colonizing species on defaunated mud were generally small, tubiculous deposit feeders. These opportunistic species had rapid development, were iteroparous, had high recruitment, and a high death rate. Gaston *et al.* (1995), using EMAP datasets, analyzed the trophic structure of macroinfaunal communities in the northern Gulf of Mexico. They reported that detritivores, including subsurface deposit feeding polychaetes, and filter-feeding bivalves living at the sediment-water interface numerically dominated the benthos in northern Gulf of Mexico estuaries. Carnivorous nemerteans and the polychaete, *Sigambra tentaculata* dominated fine textured habitats in Louisiana benthic assemblages.

Gaston and Nasci (1988) and Gaston *et al.* (1988) studied macroinfaunal communities in Calcasieu Estuary, Louisiana. Macroinfaunal assemblages were dominated by deposit-feeding species which were primarily polychaetes. Surface-deposit feeders were dominant in upper estuary, subsurface-deposit feeders dominated the lower estuary, and a mixed assemblage was found in the middle estuary. Periodic shifts in species dominance occurred within each region, but these shifts were without temporal pattern and seldom led to changes in trophic structure. The macroinfaunal assemblage of the upper estuary was dominated by early colonizing species which switched feeding mode with changes in riverine discharge, suggesting that disturbances had an effect on structuring the benthic communities.

Kalke and Montagna (1991) studied the effects of freshwater inflow on macrobenthos in riverine and bay macroinfaunal communities in Texas. Sediment grain size did not have an effect on the spatial distributions of benthic species. Most variation in spatial distributions could be explained by changes in riverine inflow. During high inflow years, freshwater and low salinity species extended their ranges into the upper bay. The high inflow was necessary to induce recruitment of low salinity species into upper bay regions. Brackish water chironomid larvae and the polychaete, *Hobsonia florida,* increased in density four weeks after a high inflow event. In contrast, the bivalves, *Mulinia lateralis* and *Macoma mitchelli,* increased densities during low inflow periods which resulted in higher benthic biomass. The polychaetes, *Streblospio* and *Mediomastus* were also positively correlated with increasing salinity during low flow periods. The amount, timing, and inter-annual variation of freshwater inflows influenced both the spatial and temporal abundance and biomass of benthic macrofauna.

Dauer and Simon (1976), Dauer *et al.* (1981), and Dauer (1985) studied the ecology of several opportunistic spionid polychaetes in Chesapeake Bay. *Paraprionospio* and other spionid polychaetes were widely distributed and rapidly colonized disturbed shallow marine and estuarine habitats. Gaston (1987) studied the feeding biology of polychaetes of the Middle Atlantic Bight. He found that the distribution and abundance of surface deposit feeding polychaetes were regulated by food resources from water-column production, while the distribution of sessile polychaetes was limited by physical disturbances. The abundance of carnivores was greatest in coarser sediments and decreased with water depth across the continental shelf; surface deposit feeders dominated most habitats and decreased across the continental shelf and increased at the shelf break. This pattern corresponded to the pattern of water column production. Subsurface deposit feeders were more abundant in fine-textured sediments and increased with depth and percent organic carbon across the shelf. Sessile polychaetes inhabited physically stable substrates and their abundance was correlated with percent silt/clay and percent organic carbon in the sediment.

Hypoxia occurs commonly during summer and early fall months on the inner continental shelf of the northern Gulf of Mexico. Freshwater runoff from rivers (especially the Mississippi and Atchafalaya) leads to density stratification of the water column and the elimination of oxygen exchange between surface and bottom waters. Additionally, decomposition of detritus increases the biological oxygen demand (BOD) of the sediments and further decreases the dissolved oxygen content of near-bottom waters. Rabalais *et al.* (1991) reported that hypoxia was a common occurrence from April to October on the inner and middle continental shelf in northern Gulf of Mexico and could cover up to 9500 km^2 during summer months off the Louisiana coast. Stratification was directly correlated with hypoxia, and reaeration of bottom waters was controlled by physical processes that were influenced by regional wind fields, river discharge, and continental shelf scale patterns. Boesch and Rabalais (1991) reported that recovery of an offshore macroinfaunal assemblage from hypoxia was rapid because the community was kept in an early successional state by the annually recurring hypoxia.

Dauer *et al.* (1992) studied the effects of hypoxia on benthic macroinfaunal in the lower Chesapeake Bay and several tributaries. Hypoxia-affected stations were characterized by lower species diversity, lower biomass, a lower proportion of deep-dwelling biomass, and changes in community composition. They observed a greater dominance by opportunistic species (euryhaline polychaetes) and lower dominance of equilibrium species (long-lived bivalves and maldanid polychaetes) at hypoxia affected stations. Benthic species exhibit varying levels of tolerance to hypoxia. Generally, polychaetes are the most tolerant taxa, followed by bivalves and amphipods (Diaz and Rosenberg 1995). The polychaetes, *Streblospio benedicti* and *Paraprionospio pinnata,* are consistently found in hypoxia-stressed habitats. Llanso (1992) found that spatial and temporal patterns in benthic macroinfaunal assemblages of the Rappahannock River could be explained by intermittent hypoxia. The benthic assemblages were dominated by opportunistic polychaetes and the response to hypoxia was species specific. The polychaetes, *Streblospio* and *Mediomastus,* became locally extinct under hypoxia, while *Loimia* and *Paraprionospio* were present in affected habitats throughout recurring hypoxia. Llanso (1991) studied the tolerance of several species of polychaetes to hypoxia and anoxia in the laboratory. *Streblospio* is an opportunistic species common in surface sediments of estuarine intertidal and subtidal habitats often exposed to hypoxia or anoxia during summer months. Under hypoxia in the laboratory, *Streblospio* adults survived 2 weeks without significant mortality, while all adults died within 55 hours under anoxic conditions. Feeding ceased and burrowing activities were both reduced under hypoxia and anoxia. Llanso (1991) postulated that field populations may survive intermittent periods of hypoxia, but the intensity and duration of low DO events may be more critical to survivorship and local population persistence.

Dardeau *et al.* (1985) reviewed the literature on macrobenthic communities in the northern Gulf of Mexico. They reported that benthic macroinfaunal populations varied seasonally and numerical abundance and species richness usually peaked between fall and spring and declined in the summer. This pattern resulted from interactions among summer hypoxia, recruitment dynamics of benthic taxa, and predation by young-of-the-year fishes entering the estuary in the spring. Gaston (1985) reviewed the effects of hypoxia on benthic communities on inner continental shelf of Louisiana. Populations of most benthic species were drastically reduced after hypoxic events. In fine sediment habitats dominated by polychaetes, the most seriously affected taxa were tubiculous and surface-feeding species, while burrowing polychaetes were more tolerant. Defaunated bottoms were rapidly recolonized after hypoxia by the polychaete, *Paraprionospio pinnata*.

Harper *et al.* (1991) studied the recovery of a benthic community at 15 m and 21 m depths to a hypoxic event during 1979 in the northwestern Gulf of Mexico. Before the hypoxic event, dominance by the polychaete, *Paraprionospio pinnata*, was declining and abundance of the amphipod, *Ampelisca* was increasing. However, the hypoxic event eliminated *Ampelisca* and there were irregular post-hypoxia eruptions of *P. pinnata* which briefly dominated the benthos. Recovery at the two sites to the hypoxic event was different: 1) the deeper water assemblage stabilized within a year - polychaetes that were dominants before the hypoxic event quickly returned to dominance and there was little evidence of succession of different species during recovery; and 2) the shallower water assemblage underwent a more complex recovery - polychaete dominance (primarily *P. pinnata*) was greatly reduced after the event and there was a successional dominance which involved several species in different taxa - each species underwent a bloom and was numerically dominant for 1-3 months, declined, and was replaced by another species bloom - polychaetes eventually regained numerical dominance two years after the hypoxic event. Generally, the macroinfaunal assemblage of hypoxia-stressed habitats in the northern Gulf of Mexico have shifted to a dominance by younger, smaller, and shorter-lived species.

Gaston and Edds (1994) analyzed the effects of brine discharge from an offshore diffuser in Louisiana on benthic macroinfaunal from 1981-1989. Brine impacts were minimal because fine sediments around brine diffuser were numerically dominated by opportunistic species (primarily estuarine polychaetes) that exhibited natural temporal and spatial fluctuations in abundance. The fluctuations in species abundance resulted from summer hypoxia and anoxia and not from brine effects. Hypoxia eliminated some taxa and severely reduced the abundance of most benthic species. They found that the only significant differences between benthic assemblages near the diffuser and those outside the influence of the discharged brine resulted from water column mixing by the discharged brine which oxygenated waters around the diffuser and stabilized the salinity of the bottom water at stations near the diffuser. This enhanced benthic diversity around the diffuser and resulted in more abundant populations during some seasons. Gaston and Edds (1994) reported that the dominant species throughout study were the polychaetes, *Paraprionospio pinnata*, and *Magelona* sp. Other species, including several polychaetes and a phoronid, were dominant during the early years of the study but densities declined to near zero during the later years. Other opportunistic species increased in abundance over the course of the study. Shifts in dominant taxa are common in many continental shelf macroinvertebrate communities. Large molluscs and other equilibrium species were never collected. Juveniles of bivalve, *Mulinia lateralis*, dominated the benthos in some years during the late winter/spring seasons, but were always eliminated by summer hypoxia/anoxia. The densities of other bivalve taxa were dramatically reduced during hypoxia/anoxia.

Boesch and Rosenberg (1982) proposed a model for the response of marine benthic communities to environmental stress on the basis of their resistance to and resilience following a disturbance based on research from northeastern United States nearshore and offshore habitats. Benthic communities in less-constant environments (*e.g.* shallow water estuaries) are more resistant because they are composed of eurytolerant species and have greater reproductive potential than communities in constant environments. After a disturbance in unstable environments, initial colonists come from a pool of species already abundant in the community, whereas initial colonists in stable habitats were often not previously dominant in community. Opportunistic species which were abundant in highly disturbed coastal habitats were largely similar worldwide, irrespective of depth and temperature. The authors concluded that resistance to stress was effective only at the individual or population level.

Diaz and Rosenberg (1995) proposed a modeling paradigm for the response of marine macroinfauna to the spatial and temporal occurrence of hypoxia. Benthic communities that experience seasonal hypoxia/anoxia, such as those off the Louisiana coast, exhibit mass mortality, are typically dominated by opportunistic species, and exhibit wide seasonal and year-to year fluctuations in species abundance related to the availability of recruits. Benthic communities that experience only periodic occurrences of hypoxia/anoxia are dominated by stress tolerant species; sensitive fauna have been eliminated so there is no mass mortality.

RECOMMENDATIONS

We feel that there is little modification that can be done to the annual monitoring program without jeopardizing the biological and statistical integrity of the dataset. It would be feasible to drop one of the four seasons of sampling without adversely impacting the present dataset. The winter and fall seasons are similar with regards to hydrography and macroinfaunal assemblages. Because of logistical difficulties in field collections, we recommend that the winter season be dropped from the sampling program. The spring, summer, and fall seasons encompass the majority of biological and physical processes that structure the benthic communities at the four LOOP sites.

To our knowledge, the LOOP monitoring program represents one of the longest and most continuous hydrographic and benthic macroinfaunal datasets collected from the northern Gulf of Mexico. This dataset will be useful for determining the long-term effects of physical and anthropogenic influences on hydrography and macroinfaunal assemblages from an array of inland, nearshore, and offshore habitats. This dataset will also provide insights into the ecological properties of benthic communities and more general questions of ecosystem stability and resiliency. The dataset permitted an evaluation of impacts of LOOP activities in relation to natural background variation in physical and biological variables. There were no significant impacts due to LOOP's operations at any of the four sites. Both control and monitoring stations at these sites exhibited seasonal and year-to-year fluctuations in hydrography, species abundance, and assemblage composition that were typical of marine communities in the Gulf of Mexico. The complex interactions and annual variation in riverine discharge, climatological patterns, and hypoxia/anoxia in the northern Gulf of Mexico contribute to the variability seen at the four LOOP study sites.

LITERATURE CITED

Boesch, D.F. 1972. Species diversity of marine macrobenthos in the Virginia area. Chesapeake Science 13: 206-211.

Boesch, D.F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Mar. Biol. 21: 226-244.

Boesch, D.F. and R. Rosenberg. 1982. Response to stress in marine benthic communities. Chapter 13. **In**: G.W. Barrett and R. Rosenberg, eds. Stress Effects on Natural Ecosystems. John Wiley and Sons, New York.

Boesch, D.F. and N.N. Rabalais. 1991. Effects of hypoxia on continental shelf benthos: comparisons between the New York Bight and the Northern Gulf of Mexico. pp. 27-34. **In**: Tyson, R.V. and T.H. Pearson (eds). Modern and Ancient continental Shelf Anoxia. Geological Society Special Publication No. 58, Geological Society Publishing House, Bath, UK.

Dardeau, M.R., R.F. Modlin, W.W. Schroeder and J.P. Stout. 1985. Estuaries. Chapter 14. **In**: Hackney, C., S. M. Adams and W.H. Martin (eds.). Biodiversity of the Southeastern United States: Aquatic Communities. John Wiley and Sons, New York.

Dauer, D.M. 1985. Functional morphology and feeding behavior of *Paraprionospio pinnata* (Polychaeta: Spionidae). Mar. Biol. 85: 143-151.

Dauer, D.M. and J.L. Simon. 1976. Repopulation of the polychaete fauna of an intertidal habitat following natural defaunation: species equilibrium. Oecologia 22: 99-117.

Dauer, D.M., C.A. Maybury and R.M. Ewing. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. J. exp. mar. Biol. Ecol. 54: 21-38.

Dauer, D.M., A.J. Rodi, Jr., and J.A. Ranasinghe. 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. Estuaries 15: 384-391.

Diaz, R. and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioral responses of benthic macrofauna. Oceanography and Marine Biology: an Annual Review Volume 33, (in press).

Gaston, G.R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. Est. Coast. Shelf Sci. 20: 602-613.

Gaston, G.R. 1987. Benthic Polychaeta of the Middle Atlantic Bight: feeding and distribution. Mar. Eco. Prog. Ser. 36: 251-262.

Gaston, G.R. and J.C. Nasci. 1988. Trophic structure of macrobenthic communities in the Calcasieu Estuary, Louisiana. Estuaries 11: 201-211.

Gaston, G.R. and K.A. Edds. 1994. Long-term study of benthic communities on the continental shelf off Cameron, Louisiana: A review of brine effects and hypoxia. Gulf Res. Reports 9: 57-64.

Gaston, G.R., D.L. Lee and J.C. Nasci. 1988. Estuarine macrobenthos in Calcasieu Lake, Louisiana: community and trophic structure. Estuaries 1: 192-200.

Gaston, G.R., S.S. Brown, C.F. Rakocinski, R.W. Heard and J.K. Summers. 1995. Trophic structure of macrobenthic communities in northern Gulf of Mexico estuaries. Gulf Research Reports 9: 111-116.

Harper, D.E., L.D. McKinnery, J.M. Nance and R.R. Salzer. 1991. Recovery responses of two benthic assemblages following an acute hypoxic event on the Texas continental shelf, northwestern Gulf of Mexico. pp. 49-64. **In**: Tyson, R.V. and T.H. Pearson (eds). Modern and Ancient continental Shelf Anoxia. Geological Society Special Publication No. 58, Geological Society Publishing House, Bath, UK.

Kalke, R.D. and P.A. Montagna. 1991. The effect of freshwater inflow on macrobenthos in the Lavaca River Delta and upper Lavaca Bay, Texas. Contr. Mar. Sci. 32: 49-71.

Llanso, R.J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Streblospio benedicti* (Webster). J. Exp. Mar. Biol. Ecol. 153: 165-178.

Llanso, R.J. 1992. Effects of hypoxia on estuarine benthos: the lower Rappahannock River (Chesapeake Bay), a case study. Est. Coast. Shelf Sci. 35: 491-515.

McCall, P.L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35: 221-266.

Rabalais, N.N., R.E. Turner, W.J. Wiseman Jr., and D.F. Boesch. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. pp. 35-47. **In**: Tyson, R.V. and T.H. Pearson (eds). Modern and Ancient continental Shelf Anoxia. Geological Society Special Publication No. 58, Geological Society Publishing House, Bath, UK.

SAS Institute, Inc. 1994. JMP Version 3.1 Statistical Software for the Macintosh. SAS Institute, Inc., Cary, N.C.